Quantitative and theoretical analysis of species distribution models for invasive species risk assessment and management

A thesis submitted in partial fulfilment
of the requirements for the Degree of
Doctor of Philosophy

at
Lincoln University
by
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Lincoln University
2017

Para mi familia luchadora.

“Je lutte donc je suis”

Author unknown

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Biological invasions are a major component of global change leading to numerous impacts on biodiversity, natural and managed ecosystems and natural resources. Despite being more vulnerable to biotic exchange, freshwater ecosystems have tended to receive less attention in invasive species research. There is an urgent need to maintain freshwater ecosystem ecological quality which requires a deeper knowledge about the species that may cause a biological invasion, as well as the process of invasion. To prevent and mitigate the effects of invasive species, biosecurity systems have been implemented in all trading nations around the world. In such systems, the estimation of species potential distribution is key to invasive species risk assessment, and decision making around that risk. Species distribution models (SDM) are therefore important tools used for early detection and are helpful for the design of improved programs for management of such species. However, these models rely on a number of assumptions that may not be valid for all species and all taxa, and there are concerns about the reliability of model predictions in new areas. The main aim of this research was to investigate the key assumptions that underlie the use of species distribution models, to understand their impact on predictions, and to determine the reliability of those predictions.

SDM characterize the species niche to infer predictions in new areas by relying on two main assumptions: the species niche remains unchanged during the invasion (niche conservatism) and that target species occupies all the suitable environments (species are at equilibrium with the environment). This thesis investigated whether these assumptions hold and, if they do not, how they could impact species distribution predictions. To further determine the reliability of SDM predictions in new areas, I investigated the impact of extrapolation when models are required to project into new areas, and the impact of evaluation methods on model performance on the reliability of predictions.

In contrast with previous research, and, in an attempt to achieve some generality, the current global distributions of a large number of invasive freshwater invertebrate (22), along with global climate records were used to test assumptions of niche conservatism, species equilibrium and the impact of extrapolation and methods of evaluating model performance.

The analysis of the global distributions of the 22 selected species in this research showed that 90% of the species did not conserve their native niche in invaded areas and were able to establish in novel environments in the invaded range. Contrary to other studies on other taxa, this result indicates that niche conservatism may be rare in invasive freshwater invertebrates and suggests that current predictive tools may underestimate the potential range of freshwater invertebrates in new areas.

Using nine species for which there were sufficient data over the invasion process, the equilibrium assumption was also challenged by niche analysis of each species in relation to residence time. As might be expected, species were found to progressively fill their niche in the invaded range (from 21 to 195 years) with increasing residence time. For the selected freshwater invertebrate species, the average number of years to reach equilibrium in the invaded range was 122 years which is faster than the time shown for other taxa. Moreover, using early invasion records I found that the selected species colonized environments different from those occupied in their native niche. Such results suggest that models constructed at earlier stages of invasion using only native information are likely to underestimate the species potential distribution.

Current concerns regarding the impact of extrapolation on model predictions were also confirmed where such predictions had high uncertainty. However, contrary to expectations, similar performing models showed high levels of uncertainty when predictions were interpolated. Of key interest, was the finding that most of the uncertainty was explained by how each model characterized the species response to the environment. Additionally, the limitations of current evaluation methods were demonstrated, which for some models tended to inflate their performance, thereby increasing uncertainty. In particular, the impact of initial steps in model building (pseudo-absences generation), on the ability to estimate model performance, was demonstrated.

This research highlights the importance and value of investigating species niche dynamics and their assessment before implementing species distribution models. The results showed that characterising the niche of species and niche dynamics to investigate SDM assumptions, could improve invasive species surveillance tools and contribute to invasive species risk assessments. For example, I demonstrated that information about niche conservatism can assist the prioritization of surveillance areas. Additionally, the study of niche dynamics enables the identification of species of

concern that are able to occupy novel environments as well as those that are able to spread rapidly across the invaded range. However, the analysis of the impact of extrapolation as well as interpolation showed the existing challenges of prediction in novel areas. As well, the analysis demonstrated the importance of validating models using multiple approaches to identify models that provide more reliable predictions that can be used in the early detection and management of invasive species. Conversely, because each model characterises the species response to the environment differently, a potential solution could be to combine predictions based on models having similar behaviours. Additionally, this work identified for a set of SDM, a range of model behaviour with various degrees of complexity. As well the trade-off between using complex and simple modelling techniques to characterize species distribution, was discussed.

Additionally, the finding that current evaluation methods can inflate model performance has led a proposal in this thesis, of a framework to obtain a more rigorous evaluation by stratifying datasets to evaluate model performance and generate pseudo-absences in a masked geographic background.

As a body of work this thesis clearly illustrates some of the opportunities for using more detailed analyses of species distribution data for invasive species risk assessment but also highlights the challenges associated with predicting the potential distribution of freshwater invertebrates, in particular, and thus the vulnerability of freshwater ecosystems. To reduce the uncertainty associated with our knowledge and understanding of freshwater species niche and to reduce uncertainty of prediction, this research highlights the urgent need for greater availability of more appropriate global datasets for further freshwater ecosystems studies.

Keywords: species distribution models, niche conservatism, equilibrium, model transferability, extrapolation, model behaviour, model evaluation, invasive freshwater invertebrates.

Acknowledgements

First, I would like to thank my main supervisor Assoc. Prof. Susan Worner. Sue, you gave me a life changing opportunity and allowed me to pursue my long yearned journey into research. Thank you for believing in me and for all your support throughout this journey. I learned many things from you, particularly trying to get research into practice. I feel honoured of being your last student and I am infinitely grateful for your patience.

I also would like to thank my supervisors, Assoc. Prof. Hannah Buckley, Dr. William Godsoe and Dr. Matthew Parry for all the technical and writing support. Hannah, thank you for your guidance, particularly during the writing of the thesis. Will, thank you for all the exciting discussions. Sometimes I left with many more questions; you clearly are a mind full of ideas. Matthew thank you for all your advice. Our intensive meetings always gave me encouragement and inspiration to keep pushing onwards to completing my PhD.

I would like to express my gratitude to the Ecological Informatics lab for your feedback and enriching discussions. Senait and Hossein thank you for the introduction to the world of SDM. For all the coffees and chats but also for reviewing almost my entire thesis, thank you Audrey. Thank you Mariona for all the discussions about science and “whatnots”. For all the laughs and companionship, thank you Marona.

I would like to thank the staff of BPRC for being always so helpful, thank you Andrew Holyoake, Sue Paterson, Sandy Wilson, Dianne Fyffe and Brian Kwan.

Thank you friends; you made New Zealand my home and this journey was enjoyable thanks to you. I won’t forget our trips and social gatherings.

I wouldn’t be here without the unconditional support of my family. There are no words to express my gratitude to all of you. To my parents; thank you for cultivating my curiosity and giving the example of perseverance. I would also like to thank Bruno; we started this adventure together and even though our paths took different directions, I take with me countless memories and lessons. Thank you for teaching me to keep my feet on the ground during stressful times. And finally thank you New Zealand for making me grow.

This study was funded by the European Commission (Erasmus Mundus partnership NESSIE, ref.372353-1- 2012-1- FR-ERA MUNDUS-EMA22), the Ministry of Primary Industries (MPI) of New Zealand, and the Better Border Biosecurity (B3).

Table of Contents

List of Tables

List of Figures

Chapter 1

Introduction

1.1 Biological invasions and freshwater ecosystems

A biological invasion occurs when a species is accidentally or intentionally introduced into a new area outside of its native range, usually by human action, whereby the species spreads from the area where it was introduced, potentially incurring ecological, economic and/ or human health impacts (Lockwood et al., 2007a; Simberloff, 2013). However, this more biogeographically-focussed definition overlooks other types of biological invasions. For instance, Valéry et al. (2009) argued that a native species can also become invasive within its own native range, where the modification of environments by human intervention leads to a change in their distribution and/or abundance. Thus, the human component is crucial in setting the context because most biological invasions are related to human activities, through environmental modification or the reduction of natural dispersal barriers, either by deliberately introducing species as food, biocontrol agents, or for recreational activities, or by unintentional transport.

The diversity of routes or pathways and the frequent exchanges between countries through tourism and trade continue to facilitate the spread of invasive species around the world (Pimentel et al., 2002; Lockwood et al., 2007b). Moreover, several human-driven components of global change, such as climate change, habitat fragmentation and biodiversity loss, can intensify the processes of invasion (Dukes & Mooney, 1999; Walther et al., 2009). For example, in recent years, mild winters in temperate regions have enabled the survival of ornamental plants from warmer regions, such as *Trachycarpus fortunei* (Arecaceae, H. Wendl), the Chinese windmill palm, that were not previously able to survive outdoors during winter (Walther et al., 2007). Thus, it is not surprising that biological invasions have considerably increased in recent decades. For example, in Europe, the number of invasive species establishing since 1970 has increased by 76% (Butchart et al., 2010) and in some countries, biological invasions, combined with other factors, represent one of the major threats to biodiversity, ecosystem services and natural resources (Gurevitch & Padilla, 2004; Pejchar & Mooney, 2009). Invasive species can have an effect on native biodiversity by direct interaction through herbivory, predation, competition or parasitism (Fritts & Rodda, 1998; Brown et al., 2002; Kuris, 2003; Nuñez et al., 2009) or by hybridisation (Ellstrand & Schierenbeck, 2000). Additionally, some invasive species can have an indirect impact on native species by transporting or vectoring diseases (Woodworth et al., 2005; Morin et al., 2007) or through a 'cascade effect' via food webs (Ricciardi & Macisaac, 2010) that can lead, in some cases, to species' extinction (Vermeij, 2004). Such effects of

invasions can occur at different biological levels from genetic, individual, population, community to the ecosystems level (Parker et al., 1999; Lockwood et al., 2007c).

Because invasions can occur at different biological levels and because part of ecological loss comprises indirect use values, such as ecosystem services, and non-use values (i.e., the existence value), makes any attempt to evaluate the economic impact of invasive species is a challenging task (Lockwood et al., 2007d). Nonetheless, Pimentel et al. (2002) were able to show for six countries, an estimated total loss of more than 200 billion USD per year with respect to the impact of invasive species on crops, pastures and forests. In a more recent effort to estimate the global cost of invasive insects specifically, Bradshaw et al. (2016) selected only studies that they considered reproducible, that is they had reported sources and clear methodologies. Their estimation of global costs were elevated to a minimum of 70 billion USD per year loss of goods and services that includes production of agricultural and forestry goods. Additionally, there are the health costs associated to insect-transmitted diseases that could reach 6.9 billion USD per year worldwide (Bradshaw et al., 2016). The invasion of pests and insect vectors that carry human and animal diseases have promoted disease outbreaks that have caused considerable impact on human and animal health (Lounibos, 2002; Spickler, 2010). Even the effects of a direct pest, such as two species of screw-worm fly *Chrysomya bezziana* (Vileneuve 1917, Calliphoridae) and *Cochliomyia hominivorax* (Coquerel 1858, Calliphoridae) in Australia, is estimated to be 500 million AUD per year and is only one example of the many exotic pests and diseases that affect live-stock worldwide (Australian Government Department of Agriculture and Food, 2017).

While the economic and environmental costs of invasive species in terrestrial ecosystems is relatively well known, particular attention should be given to freshwater ecosystems since, in some regions, freshwater biodiversity is declining at greater rate than in terrestrial ecosystems (Ricciardi & Rasmussen, 1999). One of the most important reasons for this decline is biotic exchange (or the introduction of invasive species) and is relatively more important for freshwater than terrestrial ecosystems (Sala, 2000). This decline is alarming as freshwater ecosystems are an essential component of global biodiversity. Freshwater ecosystems support exceptional biodiversity relative to habitat extent, holding 6% of all described species and 25% of vertebrates worldwide (Stiassny, 1996; Dudgeon et al., 2006). In addition, freshwater supplies are the most critical component for human survival and freshwater ecosystems provide basic services such as drinking water, energy, transportation corridors and irrigation for agriculture and food in many countries (Silk & Ciruna, 2005). Consequently, there is an urgent need to maintain the ecological quality of freshwater ecosystems and that requires a great deal of knowledge about the species and processes within such systems, but also an understanding of biological invasions in those systems (Francis & Chadwick, 2012).

Freshwater ecosystems are affected by both unintentional and intentional introductions of species for commercial use (aquaculture) and release of organisms for recreational activities and biological control (Silk & Ciruna, 2005; Francis & Chadwick, 2012). Lodge et al. (1998) stated that the vectors in freshwater ecosystems that transport aquatic species are more diverse and less controlled than in terrestrial ecosystems and consist of shipments, ballast water, boat hulls and introductions associated with recreational activities. Relative to terrestrial ecosystems, freshwater ecosystems are greatly connected because water is an effective agent for the transport of humans goods and services as well as many organisms (Francis & Chadwick, 2012). Moorhouse & Macdonald (2015) discussed the lack of comparable vectors in terrestrial ecosystems where sometimes in freshwater systems, entire communities containing numerous individuals and species are transported and released. For example, one ballast water tank was shown to contain up to 240 million organisms of several species, illustrating the vulnerability of freshwater ecosystems (Silk & Ciruna, 2005). Moreover, Rahel (2007) illustrated how humans, at large scales, have increased connectivity in freshwater systems that were previously isolated by biogeographic barriers and consequently favoured the dispersal of aquatic invasive species. Thus, these systems are highly prone to biological invasions. It is therefore not surprising that many case studies from the earliest work of invasion ecology carried by Elton (1958) were on freshwater species (Francis & Chadwick, 2012). Furthermore, freshwater invasive species comprise more than 20% of species from the IUCN list of the 100 worst invasive species (Lowe et al., 2000).

Although most introductions of non-native species have negligible effects (Williamson, 1999), some can cause considerable damage. With respect to freshwater ecosystems, for example, the Eurasian zebra mussel (*Dreissena polymorpha,* Beneden 1835, Dreissenidae) is one of the worst invasive species (Lowe et al., 2000) and is known to have accelerated regional extinction rates of freshwater mussels in North America (Ricciardi et al., 1998) as well as decreasing zooplankton abundance (MacIssac, 1996). The zebra mussel has the ability to accumulate on any surface using their byssal threads causing biological biofouling. An excessive aggregation of zebra mussels can cause severe damage in water intakes and other marine structures affecting fundamental human needs (MacIssac, 1996). The economic impact of this species on drinking water and electric power generation facilities has been estimated at 267 million USD just 15 years since its discovery in North America (Connelly et al., 2007). Similarly, shell accumulation of *Corbicula fluminea* (Müller 1774, Cyrenidae), the Asian clam, can also represent a serious problem in pipes and other structures, such that their presence can lead to an increase of dredging frequency and loss of recreational and fishing areas (Ilarri & Sousa, 2012). *C. fluminea* also has an impact at different biological levels. As an ecosystem engineer, this species significantly changes lakes by modifying water clarity, light

penetration, water infiltration among other impacts, which in turn affect the communities of vegetation, plankton and benthos (Ilarri & Sousa, 2012).

Large impact in freshwater ecosystems can also be caused by microscopic species such as the Cladoceran zooplankton, *Bythotrephes longimanus* (Leydig 1860, Cercopagididae), the spiny water flea. This species has an impact on native zooplankton assemblages where species richness, abundance and biomass tend to decrease in invaded, compared to uninvaded, lakes (Strecker, 2012 and references therein). The productivity of certain layers of water in lakes has also been shown to be reduced by *B. longimanus*, which is suspected to be the result of direct predation of zooplankton and their avoidance of predation (Strecker, 2012 and references there in). In some lakes across Canada, the spiny waterflea has also displaced some native invertebrate predators (Strecker, 2012).

Another invasive species that displays a competitive interaction with native species is *Pacifastacus leniusculus* (Dana 1852, Astacidae), the signal crayfish, which can outcompete and displace other native crayfish species due to its large size, fast growth and aggressive behaviour (Dunn, 2012 and references therein). It is also suspected that this species produces chemical cues that deter other crayfish (Dunn, 2012 and references therein). Such species can also have indirect effects on local fauna. For example, *P. leniusculus* can vector an oomycete, *Aphanomyces astaci,* that causes high mortality in native crayfish populations (Dunn, 2012 and references therein).

Invasive freshwater invertebrates can be vectors of serious diseases in humans and animals. For instance, the Asian tiger mosquito, *Aedes albopictus* (Skuse 1894, Culicidae), can transmit several viruses including dengue, chikungunya, and West Nile virus. *A. albopictus* is considered the main vector of dengue in epidemics on Reunion Island during the 1970s where 30% of the population was affected (Reiter et al., 2006; Leisnham, 2012). In addition, it was recorded as the main vector of chikungunya virus in several outbreaks in the Indian Ocean, central Africa and Italy (Reiter et al., 2006; Leisnham, 2012).

Additionally, some freshwater invertebrates can become serious economic pests, such as *Pomacea canaliculata* (Lamarck 1819, Ampullariidae) in irrigated rice agriculture in several countries in Asia (Cowie & Hayes, 2012, and references therein). This snail can also have severe impacts on native aquatic plants (Collier et al., 2011). *P. canaliculata* can also carry parasites such as the rat lungworm, a nematode that causes human fatalities through eosinophilic meningoencephalitis (Cowie & Hayes, 2012, and references therein).

To mitigate potential impacts of invasive species, biosecurity systems are implemented by governments around the world. Biosecurity includes a wide range of pre-border, border and post-border interventions to prevent and manage biological invasions. In addition to prevention,

surveillance is one of the most important components of a biosecurity system because it ensures the early identification of biosecurity threats when cost-effective interventions can still be implemented (Hellström, 2008). Surveillance is the process of collecting and recording data of invasive species occurrence or absence through surveys and monitoring procedures (Jarrad et al., 2015). For early detection, regular surveys are needed to detect the species at the earliest time possible and to trigger a rapid response. The surveys are organized to look for specific species or to survey a particular area of high value, such as a conservation area. Identifying regions that are potentially at high risk of invasion is therefore crucial such that they can be kept under close surveillance. Thus, an estimation of the potential distribution of invasive species is necessary to implement such measures.

Models can be used to predict "what should be observed in a particular system before making the actual observation" (Mouquet et al., 2015). These tools have proven to be essential to target surveillance and management measures, particularly, in areas where they are not yet present or where they have a limited distribution. Generating models on the potential distribution of a species also comes with several challenges, such as which ecological, environmental and evolutionary factors to include, as well as uncertainties associated with model predictions (Venette et al., 2010) . Models represent an ecological system based on different hypotheses but often rely on a unifying theory that needs to be clearly stated.

1.2 Niche and species distribution models

Describing the distribution of any species in its native or invaded range relies on the niche concept which was first defined by Grinnell (1917) as the combination of environments where a species can live. Following the Grinnell (1917) description of a species niche, other views emerged, such as that of Elton (1927), who proposed that a species niche is only related to the presence of resources and biotic interactions. Soberón (2007) argued that both classes of niche (Grinellian and Eltonian) are important for characterizing the distribution of a species, the main difference depending on the scale at which the influential factors are measured. Several authors discussed theories of a hierarchical organization where Grinnellian niches are measured at large spatial scales, whereas Eltonian niches are measured at smaller spatial scales (Pearson & Dawson, 2003; Soberón, 2007). Both niche definitions were later formalized by Hutchinson who considered a niche as an n-dimensional hypervolume defined by the factors that allow a species to survive and persist (Hutchinson, 1957).

Hutchinson also made a distinction between the fundamental niche and the realized niche. The fundamental niche is delimited by the species physiological requirements along the environmental factors. Whereas the realized niche represents the environments where a species lives when it is coexisting with other species. In general, the realized niche is a portion of the fundamental niche, although in some cases positive interactions can act to increase the

environments that can be tolerated. More recently, Soberón and Peterson (2005) redefined the realized niche by including environments that are accessible to the dispersal capabilities of the species. This framework that now includes movement along with biotic and abiotic factors, called BAM (biotic, abiotic and movement) (Figure 1.1), is the most commonly accepted definition of the realized niche in the context of modelling species distributions.

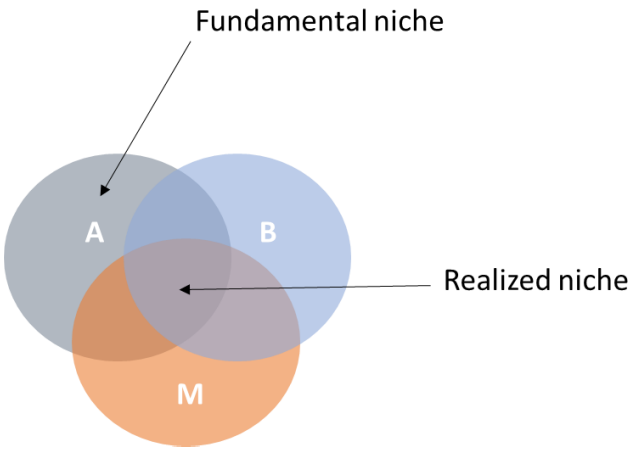


Figure 1.1 The BAM diagram by Soberón (2007). A represents the abiotic conditions where a species can survive. B represents the conditions where a species can coexist with other species and M represents the accessible areas where a species can disperse. The realized niche is at the intersection of these three components.

The fundamental and realized niche are the underlying concept of species distribution models (SDM). These models and their resulting maps have demonstrated their potential for modelling the distribution of suitable environments, thus providing support for making invasive species management decisions. For example, SDM are usually included in several pre-border and post-border risk assessments to guide decisions about which species can be imported and to identify widespread already-established invasive species (Leung et al., 2012). SDM also are used to make decisions in other fields such as conservation or epidemiology. For instance, the critical habitat for four threatened bird species was identified in Spain and outputs were later considered in the Natura 2000 network management plan (Guisan et al., 2013)

The most common approach is the correlative SDM, which associates occurrence data with environmental variables using a response function (Guisan & Zimmermann, 2000). The other main type of SDM is mechanistic, where sites that are environmentally suitable are characterized through a mathematical function describing life history traits, such as development, growth, reproduction, and/or functional traits such as morphology, behaviour or physiology (Dormann et al., 2012). There is not always a clear dichotomy between these two approaches. In some cases, correlative SDM can include ecological processes, for example, hybrid-models (see Gallien et al., 2010 for a review on the

topic) and sometimes mechanistic models can use occurrence data for estimating model parameters, e.g., CLIMEX (Sutherst & Maywald, 1985). Mechanistic models can require extensive knowledge from complex experimentation or observation. Such data is often limited in availability, particularly for poorly-known invasive species. In in the context of surveillance, this type of approach is impractical as a large number of species need to be considered. Correlative models, however, are based on occurrence data that are relatively easy to acquire. A development in recent years that facilitates modelling studies is that occurrence information is being more frequently shared in global databases such as the Global Biodiversity Information Facility (http://www.gbif.org), CITES species database (http://www.cites.org), and iNaturalist (http://www.inaturalist.org).

There is still an ongoing debate on the appropriate name for SDM, also known as 'ecological niche models' or 'habitat suitability models' (Araujo & Peterson, 2012; Warren, 2012; McInerny & Etienne, 2013). Most of the debate is centred on whether to include the term 'niche' when using occurrence data as niche refers to the interaction of abiotic, biotic and dispersal factors, which are not all explicitly included in the modelling process. Throughout this work, I choose to use the terminology 'species distribution models' to refer to the statistical formalization of the realized niche that is successively projected in the geographic space. The term 'niche' is used when referring directly to the hypervolume of environmental conditions where a species can survive, which is characterized in the environmental space (or niche space) (Hutchinson, 1957).

1.3 Factors affecting distribution patterns of freshwater invetebrates

The distribution patterns of any species are strongly related to the scale at which they are observed, i.e., the grain size and extent. The factors affecting the distribution, and thus the niche, are organized into a hierarchical structure where abiotic conditions act at large scales and biotic interactions at smaller scales (Pearson & Dawson, 2003; Wiens, 2011). In this work, more focus is given to large-scale distributional patterns, thus, only abiotic factors affecting freshwater invertebrates are considered here.

One of the most important abiotic factors limiting freshwater invertebrates is water temperature (Macan, 1961; Hynes, 1970; Hershey et al., 2010). As ectotherms, such species do not regulate their temperature and depend on external conditions to regulate their metabolism. Temperature can modify oxygen solubility and fluid, thereby indirectly affecting some life history traits (Hershey et al., 2010). Precipitation can also drive species' critical limits; changes in precipitation affects stream runoff and flood regimes, which can modify the biotic habitat, having a direct effect on invertebrate communities (Milly et al., 2005; Death, 2008).

Water chemistry such as pH, salinity and other elements can also play a crucial role in delimiting the distribution of freshwater invertebrates. For example, *Eriocheir sinensis* larvae live in high salinities, whereas the adults are found in freshwater and migrate to estuaries in order to breed (Bentley, 2012). Other invertebrates such *Corbicula fluminea* require a certain concentration of calcium in order to generate their shells (Ilarri & Sousa, 2012).

Only regional databases exist for many important freshwater variables (e.g., Chee & Elith (2012), https://teamwork.niwa.co.nz) or the data come from individual stations which are not interpolated on a regular grid (e.g., http://daac.ornl.gov). However, global information on climate variables such as air temperature, soil radiation and precipitation are readily available and were used in this study (http://www.worldclim.org/, https://www.climond.org/). Air temperature is frequently used as a proxy of water temperature for a clear link between air and water temperature has been found (Caissie, 2006).

1.4 The challenge of predicting species distribution

Our ability to predict species' distributions is challenged by the fact that ecological processes are dynamic. First, species fundamental and realized niches can change during the process of invasion. Second, historical factors, such as residence time, will affect the degree to which species fill their niche in introduced areas. Moreover, some aspects of model behaviour will affect predictions in new areas but those effects are still poorly understood. In addition, there are some issues with current methodologies of model evaluation that undermines the identification of models able to generalize species response to environmental factors. The challenges mentioned above will be briefly explained in the following sections.

1.4.1 Niche conservatism

The identification of potential areas of species distribution would be straightforward if species were static organisms. Indeed, a major assumption when using SDM is that the species niche is conserved. In other words, niche conservatism is the tendency for the species environmental requirements to remain unchanged over time (Peterson et al., 1999; Pearman et al., 2008). In the context of biological invasions, niche conservatism means that species occupy the same environments in both their native and introduced ranges. However, there is good evidence that during the invasion process, some species depart from their fundamental or realized niche, thereby exhibiting niche shifts (Alexander & Edwards, 2010). Indeed, Guisan et al., (2014) reviewed the frequency of these changes in invasive species and found that from 180 species, 50% of the cases indicated a niche shift (29% animals and 21% plants).

During the process of invasion, some species are released from their natural enemies (predators, parasites) or competitors and are able to colonize environments from which they were excluded in the native range resulting in a realized niche shift (Keane & Crawley, 2002). In other situations when species are confined within a geographic range and transported in new areas, they can also show a realized niche shift by occupying new environments for which they were pre-adapted (Dlugosch & Parker, 2008). Also, adaptive responses can occur as a result of genetic change when populations in the invaded range are isolated from gene flow from the native range which will favour emergent adaptation (Kirkpatrick & Barton, 1997). Similarly, multiple introductions from several source populations or admixture of previously isolated native populations can introduce genetic novelty which could lead to fundamental niche shift (Blows & Hoffmann, 2005). Phenotypic plasticity may also enable the colonization of new environments by allowing a certain genotype to survive in these environments. Phenotypic plasticity can result in a realized niche shift but sometimes in a fundamental niche shift provided the trait is selected (Levin, 2009).

Whether species conserve their niche during the invasion is a question of critical importance as it undermines some of the uses of species distribution models and climate matching particularly for invasive species risk assessments (Guisan et al., 2014). First, the risk areas are likely to be underestimated if a niche shift is taking place. Second, the detection of a niche shift will invalidate the use of climate matching with only the native range as done in some invasive species risk assessments (Kumschick & Richardson, 2013). Thus, detecting which species are going through a niche shift can provide insight on the reliability SDM predictions and add new knowledge for the assessment process. Investigating niche shifts will also allow us to identify species that show ecological or evolutionary responses that allow them to colonize new environments. Moreover, from a fundamental perspective, assessing the frequency at which such shifts occur for freshwater invertebrates will provide insights on the ecological responses of these organisms and the potential vulnerability of freshwater ecosystems. Other organisms such as Holarctic terrestrial plants and birds have indicated a prevalent niche conservatism (Petitpierre et al., 2012; Strubbe et al., 2013), whereas for amphibians, reptiles and marine fishes, niche shifts were more prevalent (Li et al., 2014; Parravicini et al., 2015). Yet, studies on invasive freshwater invertebrates have focused on only a few species (e.g., Loo et al., 2007; Larson et al., 2010; Medley, 2010; Gallardo et al., 2013), which impedes the possibility of generalizing about niche conservatism for these organisms.

1.4.2 Residence time and climatic equilibrium

Species distributions are not solely dependent on suitable conditions. Indeed, residence time will also determine whether species achieve their full geographic extent. In fact, several studies have established that species range size within the introduced range will increase with longer residence

time (Wilson et al., 2007; Williamson et al., 2009; Byers et al., 2015). Observed species distribution limits are likely to represent only a mere glimpse of the species' niche because there has not been enough time for it to fully occupy its potential niche. Thus, residence time is going to determine whether a species' distribution is in equilibrium. A species is in equilibrium when it occurs in all suitable locations and is absent in all unsuitable locations (Araújo & Pearson, 2005). Such an equilibrium is frequently assumed when using SDM. However, currently, there is no information on how long it takes for freshwater invertebrates to reach a potential equilibrium. Moreover, investigating the dynamics of species' niche dynamics can also increase our understanding on invasions. What types of environments are occupied at initial stages of invasions and at what rates do species spread? Yet most of the studies use only static information on species distributions. It is therefore important to investigate how a species' niche changes with increasing residence time and when it is likely to reach equilibrium in a given environmental situation.

1.4.3 Extrapolation

The estimation of suitability in new locations is obtained by model interpolation and extrapolation. The use of each approach will depend on whether the new location is characterized by environmental conditions that are inside (interpolation) or outside (extrapolation) the calibration data range. There is a widespread concern about the validity of predictions when they are obtained by model extrapolation (Fitzpatrick & Hargrove, 2009) because a species' response to environmental conditions that are outside of the calibration range is unknown. Consequently, no information is available to validate model predictions under these novel conditions. As a result, several authors have recommended the reporting of locations where extrapolation is occurring to indicate uncertain predictions (Fitzpatrick & Hargrove, 2009; Elith et al., 2010; Owens et al., 2013). However, model extrapolation is sometimes necessary. A good example is when SDM are used to predict distributions under climate change where novel conditions will be observed. Extrapolation can be used provided models are inferring sensible species' response to environmental conditions. Model behaviour has been investigated for some widely-used models by Elith and Graham (2009), however determining if other models are showing sensible extrapolation behaviour needs to be further investigated. Also there is a lack of empirical evidence as to whether predictions obtained by model extrapolation are uncertain. Clearly, given the importance of making assessments of invasion risk in new environments, a closer examination of model behaviour and uncertainty around extrapolation is needed.

1.4.4 Towards an improved assessment of model transferability

Model transferability refers to the ability of models to generalize species' responses to environmental conditions. Traditionally a model's ability to generalize is quantified by measuring errors in predictions on test datasets. Ideally, an independent dataset from the calibration dataset is

needed to properly test model transferability (Elith et al., 2006). Since these datasets are rarely available, most studies test their models by randomly dividing the available dataset into a calibration and test dataset. However, by using this approach, there is no guarantee that both calibration and test datasets will be independent. First, some locations present in both datasets are sometimes spatially close together and, therefore, will tend to be similar to each other (Bahn & McGill, 2013). Second, I expect that a dependence between the two datasets can arise when pseudo-absences are generated using occurrence information (see 2.2.5.1 Chapter 2 for information on pseudo-absences). A dependence between the calibration and test dataset will result in biased model evaluation. More investigation is needed to understand how performance measures are affected by the dependence between the calibration and test dataset and to identify a better approach to evaluate model performance.

1.4.5 Using New Zealand to showcase the challenges of species distribution prediction

Historically, New Zealand has endured significant impact from biological invasions since Europeans settled there in the early 19th century. Invasions into New Zealand are believed to have been facilitated by its temperate marine climate, the absence of significant natural enemies and the expansion of human-transformed habitats (Lee et al., 2006). The devastating effect of biological invasions on its native biota and productive ecosystems gave rise to the establishment of one of the most comprehensive biosecurity systems in the world. New Zealand's biosecurity system involves close collaboration between multiple parties such as government departments and research institutions and interventions against invasive species are implemented at several instances at pre-border, border and post-border, with the aim to encompass all ecosystems. With respect to freshwater ecosystems, a report by Smith & Dodgshun (2008) identified several invasive invertebrates that could be a potential threat to New Zealand. According to Smith & Dodgshun (2008) at least four species of invasive invertebrates have a high risk of introduction to New Zealand. These species are *Aedes albopictus* (Skuse 1894, Culicidae), *Corbicula fluminea* (Müller 1774, Cyrenidae), *Eriocheir sinensis* (Milne-Edwards 1854, Varunidae) and *Cercopagis pengoi* (Ostroumov 1891, Cercopagididae). Several previous introductions of invasive invertebrates into New Zealand were the result of imported aquatic plants and the aquarium trade (Smith & Dodgshun, 2008; Duggan, 2010). For example, a live apple snail (*Pomacea diffusa*) detected in a river in the North Island in 2010 was suspected to come from an aquarium release (Collier et al., 2011). These examples highlight the need to develop and improve tools that will aid early detection and thus the challenges of species distribution prediction will be investigated using New Zealand as a case study.

1.5 Overall aim and objectives

The aim of this thesis is to use freshwater invertebrates as a case study system within which to investigate the implications of the underlying assumptions of species distribution models in distribution predictability and to address the methodological challenges of transferring distribution predictions in other areas.

The specific objectives are:

- Objective 1: To determine whether a set of invasive freshwater species have retained their native niche during the process of invasion and how niche conservatism affects species distribution models.

- Objective 2: To establish the effect of residence time on species niche dynamics and determine the necessary time for invasive freshwater species to reach equilibrium.

- Objective 3: To understand model behaviour during extrapolation and to compare the degree of uncertainty between model interpolation and extrapolation.

- Objective 4: To assess the effect of the dependence between calibration and test datasets on model performance and identify an approach to rigorously evaluate model transferability.

1.6 Thesis structure

Chapter 2 addresses Objective 1 by providing an estimation of the frequency at which invasive freshwater species conserve their niche using 22 species as case studies. It also shows the effect of niche conservatism on model performance. Finally this chapter offers a novel approach for prioritizing risk areas using niche conservatism information. Chapter 2 also contains a thorough description of the methodologies used throughout this thesis.

Chapter 3 addresses Objective 2 by illustrating niche dynamics across residence time and provides insight on the process of invasion of several species by measuring the time necessary to reach equilibrium and the rate at which species fill their niche.

Chapter 4 addresses Objective 3 by offering a thorough evaluation of uncertainty in interpolated and extrapolated predictions and provides a comprehensive study on model behaviour.

Chapter 5 addresses Objective 4 by evaluating the effect of pseudo-absence generation and model evaluation approach on model performance.

Chapter 6 synthesises the outputs of this thesis and shows how this research contributes to a deeper understanding of species invasions and species distributions models. This chapter also explains the implications of this work for monitoring and management of invasive species and provides some research directions that can be addressed in the future.

Chapter 2

Prioritizing hotspots of invasion using niche conservatism information: a case study of invasive freshwater species in New Zealand

2.1 Introduction

Biological invasions, in interaction with other factors, represent one of the major threats to biodiversity (Gurevitch & Padilla, 2004). Furthermore, in addition to biotic change, other human-driven components of global change, such as climate change and habitat fragmentation, are predicted to increase the prevalence and range of invasive species worldwide (Dukes & Mooney, 1999; Walther et al., 2009). Several studies report the dramatic increase of non-native freshwater invertebrates arrival and/or establishment in different regions of the world (Robinson, 1999; Devin et al., 2005; Roy et al., 2014). In New Zealand, there have been numerous purposeful introductions for recreational activities and aquaculture, however more recently, many introductions have been unintentional highlighting the importance of implementing effective surveillance strategies (e.g. Duggan, 2002; Duggan et al., 2006, 2014; Holder et al., 2010; Collier et al., 2011; Rowe et al., 2011). Early detection followed by a rapid control response can have considerable influence on a successful eradication (Myers et al., 2000). Therefore, identifying the environments where an introduced species is likely to thrive is of critical importance for detecting areas where surveillance, containment or eradication must be taken. Surveillance strategies are usually species specific and are focused on economic optimization and detection maximization (Dodd et al., 2016), however assessing the risk of invasion for multiple species in an area should facilitate the development of more cost effective and targeted management strategies. Also known as hotspot analysis, this approach to the detection of suitable environments for multiple species is traditionally used to identify high biodiversity areas, but has been recently applied to detect hotspots of biological invasions (e.g. O'Donnell et al., 2012; Adhikari et al., 2015). Hotspots of biological invasions can be described within biogeographic regions that encompass a distinctive set of communities with similar environmental conditions, disturbance regimes and natural barriers. Because these communities function together, an assessment of the risk of invasion by biogeographic region is likely going to facilitate management strategies.

Correlative species distribution models (SDM) are statistical models used to identify potential suitable environments for species by associating their occurrence to the prevailing environmental factors at those locations (Guisan & Thuiller, 2005; Elith et al., 2006). In general, SDM are based on theories developed by Hutchinson (1957), where a species' niche describes the combination of

environments required to support a persistent population and is represented by a hypervolume of those environmental conditions. In practice, correlative SDM capture only a portion of the fundamental niche, Hutchinson (1957) described as the realized niche which encompasses the environmental conditions to which a species is confined due to interactions with other species. Using such models to predict species' invasion probabilities into other areas relies on the assumption of niche conservatism that requires that the realized niche is conserved between the native and invaded range (Peterson et al., 1999; Wiens & Graham, 2005). However not all invasive species necessarily retain their environmental requirements from the native range, and any change in the position or the limits of the niche envelope indicates a realized niche shift (Guisan et al., 2014). It is therefore critical to detect when niche shifts occur to identify invasive species that are likely to pose problems for management because of their ability to colonize novel environments. In the context of invasion, if the species conserves the environmental preferences of their native range, a SDM should correctly identify suitable areas in the non-native range and therefore priority areas for monitoring can be easily identified. But if a niche shift has occurred, the invader's potential habitats should be considered carefully since it can establish in environments not occupied in the native range making it difficult to prioritize areas and therefore hampering its management. Niche shifts can be observed in analogous (environments present in both invaded and native ranges) and/or non-analogous environments (environments present in only one range) (Guisan et al., 2014). A much debated question is how to interpret niche shifts in non-analogous environments (Guisan et al., 2012; Webber et al., 2012), nevertheless their identification will also be of important from a management perspective. Furthermore, the importance of niche conservatism for SDM has been highlighted in several studies, Petitpierre et al.,(2012) and Strubbe et al., (2013) found a positive relationship between niche conservatism and predictive performance of SDM. In addition, information about niche conservatism is also likely to be important to consider for prioritization of surveillance areas in a target region. By identifying environments where species show niche conservatism, areas more likely to be colonized by the species can be highlighted as these environments possibly represent optimal conditions for the species establishment.

In this study, I investigate the prevalence of climatic niche conservatism in invasive freshwater invertebrates and how that information could be used in the assessment of risk areas. Using the distribution of 22 globally invasive freshwater species, I estimate for the first time the frequency of occurrence of climatic niche shifts for freshwater invertebrates. I identify hotspots of invasion in New Zealand as a case study, and use a novel approach to prioritize risk areas by combining information about niche dynamics and climate suitability. My specific objectives were to, 1) determine if invasive freshwater invertebrates have conserved their native climatic niche during invasion in both analogous and non-analogous environments, 2) assess whether niche conservatism can positively

affect the performance of SDM, and, 3) identify potential hotspots of invasion and niche conservatism for target species in New Zealand.

2.2 Methods

2.2.1 Target species and occurrence data

Twenty-two invasive freshwater species that are known to cause considerable impact in several regions of the world were selected for this study (Table 2.1) (Smith & Dodgshun, 2008; Loo, 2012). The distribution information for the 22 species was extracted from GBIF (www.gbif.org, last accessed May 5, 2014), GISIN (www.niiss.org, last accessed December 18, 2014), and collected from publications and taxon experts. For further details see Worner et al. (2010). The recommendations by Chapman (2005) for cleaning distribution data extracted from GBIF, were followed. In particular, errors were found in the coordinate systems used for USA and Canada, along with zero latitude/longitude points and countries that were wrongly labelled. All misleading points were corrected if possible or removed to avoid misleading information. The native and invaded range status for each species was delimited by country or continent (Table 2.1). The resolution for extracting environmental information was set to 10 arc minutes (0.17°) and only one occurrence point per grid cell was used to minimize spatial autocorrelation and inflation of accuracy measures (Veloz, 2009; Kramer-Schadt et al., 2013).

Table 2.1 List of species studied, their number of occurrences and respective native range.

Full name	Number of occurrences	Native range	References for native range
Aedes albopictus (Skuse, 1895)	2975	Asia	(Walton & Hoddle, ; Rochlin et al., 2013)
Bithynia tentaculata (Linnaeus, 1758)	1046	Europe	(Kipp et al., 2016a)
Bythotrephes longimanus (Leydig, 1860)	516	Europe and Asia	(Liebig et al., 2016)
Cercopagis pengoi (Ostroumov, 1891)	169	Ponto Caspian countries [1]	(Benson et al., 2016; Anonymous, 2017a)
Cipangopaludina japonica (von Martens, 1861)	46	Asia	(Bury et al., 2007; Kipp et al., 2016b)
Corbicula fluminea (O. F. Müller, 1774)	1409	Asia	(Morton, 1986; Barbour et al., 2013)
Dikerogammarus villosus (Sowinsky, 1894)	92	Ponto Caspian countries	(Aldridge, 2005; Dodd et al., 2014)
Dreissena polymorpha (Pallas, 1771)	1468	Ponto Caspian countries	(Son, 2007)
Dreissena bugensis (Andrusov, 1897)	240	Dniepr Delta countries[2]	(Son, 2007)
Eriocheir sinensis (Milne-Edwards, 1854)	1046	Asia	(Anonymous, 2009; Benson & Fuller, 2016)
Gammarus tigrinus (Sexton, 1939)	293	North America	(Boets et al., 2011; Dobrzycka-Krahel et al., 2013; Strode et al., 2013)
Hemimysis anomala (G.O. Sars, 1907)	98	Europe	(Anonymous, ; Kipp et al., 2016d)
Limnoperna fortunei (Dunker, 1857)	121	Asia	(Darrigran & Damborenea, 2003; Ghabooli et al., 2013)
Orconectes limosus (Rafinesque, 1817)	881	North America	(Pârvulescu et al., 2009; Swecker et al., 2010; Aklehnovich & Razlutskij, 2013)
Orconectes virilis (Hagen, 1870)	547	North America	(Larson, Eric R.Busack & North, 2010; Benson, 2016)
Pacifastacus leniusculus (Dana, 1852)	546	North America	(Kouba et al., 2014; Anonymous, 2016)
Pomacea canaliculata (Lamarck, 1828)	236	South America	(Cowie, 2005)
Potamopyrgus antipodarum (Gray, 1843)	1892	New Zealand	(Loo et al., 2007)
Procambarus clarkii (Girard, 1852)	490	North America	(Guerardi & Panov, 2006; Anonymous, 2017b)
Pseudodiaptomus inopinus (Burckhardt, 1913)	103	Asia	(Anonymous, 2007)
Rhithropanopeus harrisii (Gould, 1841)	158	East Coast of North America	(Anonymous, 2008; Harriet, 2016)
Valvata piscinalis (Muller, 1774)	1001	Europe	(Grigorovich et al., 2005; Kipp et al., 2016c)

2.2.2 Climatic data

Twenty-seven climatic variables associated with temperature, radiation and precipitation were extracted from Climond (Kriticos et al., 2012) at 10 arc minutes (0.17°) resolution to characterize each occurrence point (Table 2.2). At the global scale only air temperature was available, however, using this variable to represent conditions in freshwater ecosystems is standard (Lauzeral et al.,

[1] Ponto Caspian countries comprise the Russian Federation, Ukraine, Romania, Bulgaria, Kazakhstan, Uzbekistan, Turkmenistan, Tajikistan, Kyrgyztan, Iran, Georgia and Azerbaijan.
[2] Dniepr Delta countries comprise the Russian Federation, Ukraine and Belarus.

2011), particularly for well-mixed water bodies like river and streams where a high positive correlation has been found between air and water temperature (Caissie 2006).

Table 2.2 Variables extracted from the Climond database (Kriticos et al., 2012).

Code	Variables
CBIO1	Annual mean temperature
CBIO2	Mean diurnal range (mean of monthly (max temp - min temp))
CBIO3	Isothermality (CBIO2/CBIO7) (* 100)
CBIO4	Temperature seasonality (standard deviation *100)
CBIO5	Max temperature of warmest month
CBIO6	Min temperature of coldest month
CBIO7	Temperature annual range (CBIO5-CBIO6)
CBIO8	Mean temperature of wettest Quarter
CBIO9	Mean temperature of driest quarter
CBIO10	Mean temperature of warmest quarter
CBIO11	Mean temperature of coldest quarter
CBIO12	Annual precipitation
CBIO13	Precipitation of wettest month
CBIO14	Precipitation of driest month
CBIO15	Precipitation seasonality (coefficient of variation)
CBIO16	Precipitation of wettest quarter
CBIO17	Precipitation of driest quarter
CBIO18	Precipitation of warmest quarter
CBIO19	Precipitation of coldest quarter
CBIO20	Annual mean radiation (W m^{-2})
CBIO21	Highest weekly radiation (W m^{-2})
CBIO22	Lowest weekly radiation (W m^{-2}
CBIO23	Radiation seasonality (C of V)
CBIO24	Radiation of wettest quarter (W m^{-2})
CBIO25	Radiation of driest quarter (W m^{-2})
CBIO26	Radiation of warmest quarter (W m^{-2})
CBIO27	Radiation of coldest quarter (W m^{-2})

2.2.3 Geographic background for niche analysis and species distribution models

In addition to extracting climate conditions from locations where the species is known to be present, the climatic conditions of the geographic background were also extracted to characterize the available environments for the species in the native and invaded range. The geographic background is the study area limited to the available environments that the species could colonize and to which species distribution models are calibrated (Peterson, 2011). Clearly, delimitation of the geographic background plays a crucial role in niche comparison and species distribution models. In this study, I used two different methods to delimit geographic background, one for niche comparison and

another for calibrating the species distribution models. For the former, the purpose was to delimit an area where the species would naturally disperse (Peterson, 2011). In general, freshwater organism dispersal is limited by the continuity of water bodies and freshwater ecoregions reflect these natural barriers. Thus the geographic background was delimited using native and invaded distributions that overlapped with freshwater ecoregions that were defined by Abell et al. (2008).

For SDM calibration pseudo-absences are often generated in a geographic background. In a study of the effect of collinearity, Dormann et al. (2013) showed that differences in correlation structure between the training and test datasets can negatively affect model performance. Therefore in this study the background for pseudo-absence generation was delimited based on the correlation structure of the environmental variables around the presence points following methods proposed by Senay et al., (2013). The method developed by Senay et al. (2013) chooses a background with similar correlation structures between environmental variables such that the generated pseudo-absences do not negatively influence predictions. To find the appropriate distance to delimit the geographic background for each species, twenty datasets that included 27 climatic variables from Climond were extracted using different radii from the presence points (every 50 km from 50 to 1000 km). For each radius, I used principal component analysis to measure the changes in variable loading across changes in distance for the variables contributing the most to principal components (Senay et al., 2013). A change in sign in the variable loading indicates that the relationships between variables are different and therefore the optimal distance should be where the sign is consistent.

2.2.4 Niche analysis

Niches can be compared using SDM with reciprocal projections, however using an ordination method has been shown to measure niche overlap more accurately (Broennimann et al., 2012). The environmental space for each species was therefore delimited by the two first components of a principal component analysis to facilitate visualization and computation of the niche metrics (Broennimann et al., 2012). The realized climatic niche, as well as the geographic background were represented within the environmental space. This niche representation is also known as PCA-ENV (Broennimann et al., 2012; Petitpierre et al., 2012). A grid was placed over the entire environmental space to divide it into 100 by 100 cells, creating a unit less raster. The particular grid size was chosen because the niche overlap measure was shown to converge at this resolution (Broennimann et al., 2012). Following procedures established by Broennimann et al.(2012), a probability density function was constructed using a smoothed kernel estimator around the transformed scores from PCA for the environment occupied by the species, and the geographic background. A smoothed kernel estimator was used because it corrects sample bias and smooths over any gaps in the environmental niche (Guisan et al., 2014). In this study I used the default Gaussian kernel to obtain a smoothed probability

density for each cell, where each cell represents a unique set of environmental conditions(Broennimann et al., 2012). The niche dynamics of each species were characterized using five metrics (Figure 2.1). The D metric (Schoener, 1970), is a niche overlap metric modified by Broennimann et al. (2012) to account for the difference in climate availability between the native and invaded range in order to infer robust niche changes. Niche overlap is computed as follows:

$$D = 1 - \frac{1}{2}\left(\sum_{ij} |z_{1ij} - z_{2ij}|\right)$$

where z_{1ij} is the occupancy of the native environment by the species in cell *ij* and z_{2ij} is the occupancy of the invaded environment in cell *ij*. The niche overlap (*D*) metric is often used to provide statistical tests of niche equivalency and similarity (Warren et al., 2008). The niche equivalency tests whether two niches are equivalent by randomly reassigning occurrences from both invasive and native niches and then determining if niche overlap is different than overlap measured between random groups. The test comprises building a null distribution for the *D* metric by, first combining the occurrences transformed from the PCA of the species native and invasive niches, second randomly choosing two groups from the combined data and third calculating a simulated *D* metric. This procedure was repeated 1000 times to create a null distribution. If the observed *D* metric falls within the 95% confidence limits of the null distribution (one tailed test), the null hypothesis cannot be rejected. In other words, the native and invasive niche do not differ significantly. The niche similarity test evaluates whether the invasive niche is more similar to the native niche than expected by chance. For testing similarity, first, the niche centroid is randomly shifted in the native niche. The *D* metric is calculated between the simulated native niche and the observed invasive niche. This test is repeated 1000 times and if overlap (*D)* is within the 95% confidence limits of the null distribution (one tailed test), the null hypothesis cannot be rejected indicating that niche similarity is retained. In other words, the invasive niche is more similar to the native niche than expected by chance.

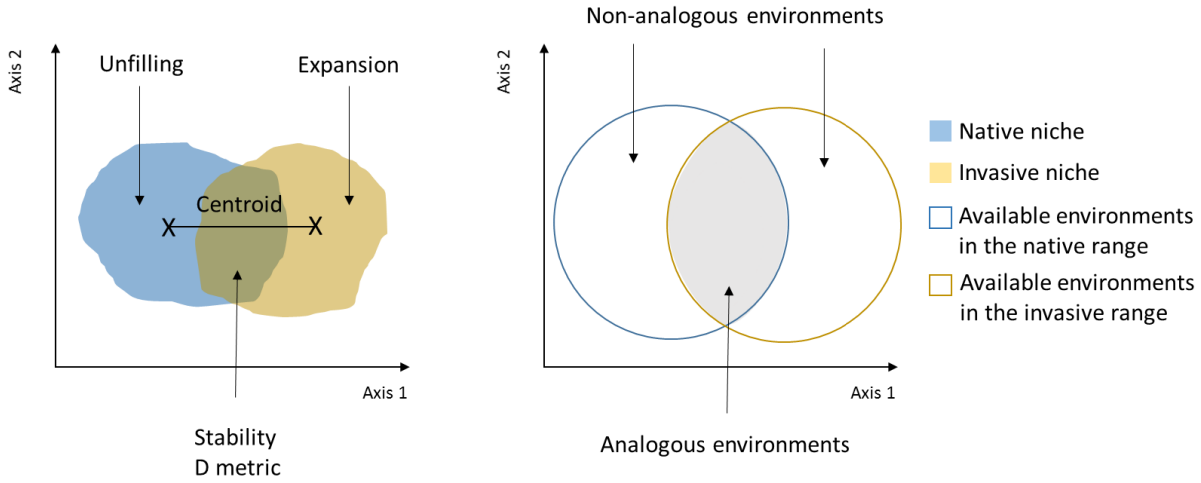


Figure 2.1 (Left) Schematic representation of the five niche metrics used to characterize niche conservatism (see section 2.2.4 for definitions). (Right) Schematic representation of analogous and non-analogous environments. The grey area shows environments that are common to both native and invaded ranges (analogous environments) while the white area shows environments existing in only one range (non-analogous environments).

Other aspects of niche dynamics were characterized using metrics developed by Petitpierre et al. (2012) (Figure 2.1). Niche stability (S) is the proportion of environments (cells) of the invasive niche shared between the native and invasive niches. Whereas expansion (E) is the proportion of environments of the invasive niche that do not intersect with native niche. Finally, unfilling (U) quantifies the parts of the species niche that are occupied in the native range and are not (yet) filled in the invasive range. To compare niche position between the native and exotic range, I created an additional index, the centroid index which compares centroid change in relation to the extent of the overall species niche. The centroid for each range is located at the median of the points. The Euclidean distance between these two centroids is computed and compared in relation to the distance that will encompass all points along the centroid line. Further details and a script are given in Appendix A.1 and A.2 respectively. All indices vary between 0 and 1; values close to 1 indicate a high overlap, stability, expansion, unfilling or centroid change.

Climate availability in invaded and native ranges is important when measuring niche changes. Some climates can be more common in the invaded range than in the native range (or conversely) and as result, false niche differentiation can be detected (Godsoe, 2010; Guisan et al., 2014). This is particularly important when some climates only exist in one range (non-analogous environments) (Figure 2.1). Thus I computed the metrics in analogous and in all environments (non-analogous and analogous environments) to identify in which type of environments niche changes are occurring. Moreover following Guisan et al. (2014) recommendations for accounting climate availability, I also computed niche metrics in the most common environments between the invaded and native range

by removing marginal climates (environments with low density). However, removing marginal climates could strongly influence the niche dynamic metrics so a sensitivity analysis, as recommended by Petitpierre et al. (2012), was carried out to determine if the metrics change with the degree of removal of marginal climates. A range of 6 percentiles was used to remove marginal climates in each range, including 75%, 80%, 85%, 90%, 95% and 100%. Two niche dynamics metrics within this range of percentiles were compared: niche expansion and unfilling following Petitpierre et al. (2012).

2.2.5 Species distribution models

2.2.5.1 Pseudo-absence generation

Because records of true absences rarely exist, pseudo absences are required to use many correlative species distribution models (SDM). The pseudo-absences are generated in the previously delimited geographic background (section 2.2.3), selecting environments that are outside of the realized niche (Worner et al., 2010; Senay et al., 2013). Compared to random pseudo-absence generation, this method reduces the chance of introducing false absences, or locations with suitable environment that could cause an underestimation of the potential distribution of the species (Iturbide et al., 2015). First the environments within the geographic background are classified to suitable and unsuitable locations using a one class support vector machine (OCSVM) algorithm (Schölkopf et al., 2001). OCSVM assesses dissimilarity between presences and locations, if the observation is too different (zero similarity to presence points) they are labelled as out-of-class and thus considered as potential pseudo-absences. Because there were many thousands of potential pseudo-absences, the final step was to group the unsuitable locations according to their environmental characteristics using a k-means algorithm (Lloyd, 1982) and by using the centroids of the k clusters to represent the environment of the unsuitable sites. The number of pseudo-absences (k cluster centroids) obtained were set to the equivalent number of presences for the species (Senay et al., 2013).

2.2.5.2 Variable selection for the prediction of species distribution

Variable selection was carried out using random forests (Breiman, 2001a), for which the most important advantages are robustness against overfitting, incorporation of predictor interactions and a measure of variable importance (Díaz-Uriarte & Alvarez de Andrés, 2006). Using random forests as a variable selection method was proposed by Díaz-Uriarte & Alvarez de Andrés (2006) where variables are selected based on their importance and minimizing out of bag (OOB) error. Variables selected for each species can be found in Appendix A.3.

2.2.5.3 Model selection and parametrization

To model species occurrence, an ensemble approach described by Araújo & New (2007) was used. Such an approach deals with model variability by combining predictions. I used nine models in a multimodel framework (Worner et al., 2014). The models were, 1) logistic regression (LOG) (McCullagh & Nelder, J. A, 1989), 2) classification and regression trees (CART) (Breiman et al., 1984), 3) conditional trees (CTREE) (Hothorn et al., 2006a), 4) k-nearest neighbours (KNN) (Altman, 1992), 5) naïve Bayes (NB) (McCallum & Nigam, 1998), 6) support vector machines (SVM) (Cortes & Vapnik, 1995), 7) artificial neural networks (NNET) (Venables & Ripley, 2002) , 8) linear discriminant analysis (LDA) (McLachlan, 1992), and, (9) quadratic discriminant analysis (QDA) (McLachlan, 1992).

Models were calibrated using both native and invasive distributions. Some of these algorithms (KNN, SVM and NNET) require a prior parameterization hence several parameters sets were tested using a 10 fold cross validation repeated 20 times. The parameters that yielded the smallest misclassification error were selected (Leday, 2008). The initial tested parameters and final parameters used for each model and species can be found in the Appendix A.4 and A.5 respectively.

A 10-fold cross validation with 200 repetitions was used to evaluate the average performance of each model using the area under the receiving operator characteristic curve (AUC) (Fielding & Bell, 1997) that has the advantage of being a threshold independent metric. The receiver operating characteristic curve (ROC) is built using all potential thresholds to obtain a binary classification. The true positive rate is plotted against the false positive rate and the area under the curve reflects the performance of the model for each species. The predictions of the different models were combined using model averaging weighted by Somers' D where $S = 2 \times (AUC - 0.5)$(Breiner et al., 2015). Accordingly, models that were outstanding in their performance were given a higher weight when calculating the average prediction (see Appendix A.6 for Somers' D results). Predictions for New Zealand were carried out using a high resolution 30 arc second Climond dataset. Averaged predictions were transformed to discrete classes (presence and absence) using the prevalence approach (Liu et al., 2005), where the threshold was set to 0.5 as the prevalence in the current study was 50% for all species. All analyses were carried out using R (R Core Team, 2015) and the list of packages used can be found in Appendix A.7.

2.2.6 Niche conservatism and model performance

To test whether niche conservatism potentially improves the performance of models predictions, correlations between niche stability, overlap, unfilling and centroid shift against average AUC were examined using Kendall's correlation test.

2.2.7 Hotspots of invasion and niche stability in New Zealand

The binary maps of all potential invasive species were overlaid to obtain hotspots of potential invasion in New Zealand. To determine niche stability climates in the geographic space, New Zealand climates were first projected within the two principal component axes used for niche comparison for each species. New Zealand locations that intersected with niche stability climates were extracted for each species and hotspots of niche stability were obtained by overlaying niche stability maps of all potential invasive species.

To facilitate conservation or biosecurity planning, I also described hotspots of potential invasion using freshwater biogeographic units. These biogeographic units were delimited by Leathwick et al.(2007) and they correspond to geographic units having similar physical disturbance regimes, colonization pathways, natural barriers and native communities of vertebrates and invertebrates. For each species, each pixel within an ecoregion was given a high risk of establishment if the pixel was climatically suitable for the species and if the climate characteristics of that pixel corresponded to the niche stability category.

2.3 Results

2.3.1 Niche conservatim in invasive freshwater invertebrates

Two species (*Dikerogammarus. villosus* and *Hemimysis anomala*) were excluded from the niche analysis as there were not enough occurrence records in their native range. For comparative purposes with other studies, a niche change of more than 10 % was considered to be significant (Petitpierre et al., 2012; Parravicini et al., 2015). When niche dynamics were measured within all environments (i.e. analogous and non-analogous environments, 90% of the species showed more than 10% of niche expansion and all species showed more than 10% of centroid change (Figure 2.2, Appendix A.8 for individual results). Niche unfilling was also prevalent where 95% of the species had at least 10% of their known niche that remained to be filled in the invasive range. However some degree of similarity was observed between invasive and native niches where most of the species showed at least 40% of niche stability but interestingly, relatively low niche overlap (*D*). Stability measures the environments (cells) that are occupied in both invaded and native ranges whereas overlap metric measures the difference in occupancy between the ranges which is likely to be large, thus giving a low *D* metric. When considering niche dynamics only in analogous climates, the overall trend remained the same where more than 80% of species indicated a change of at least 10% of centroid, niche expansion and unfilling. (Figure 2.2, Appendix A.9).

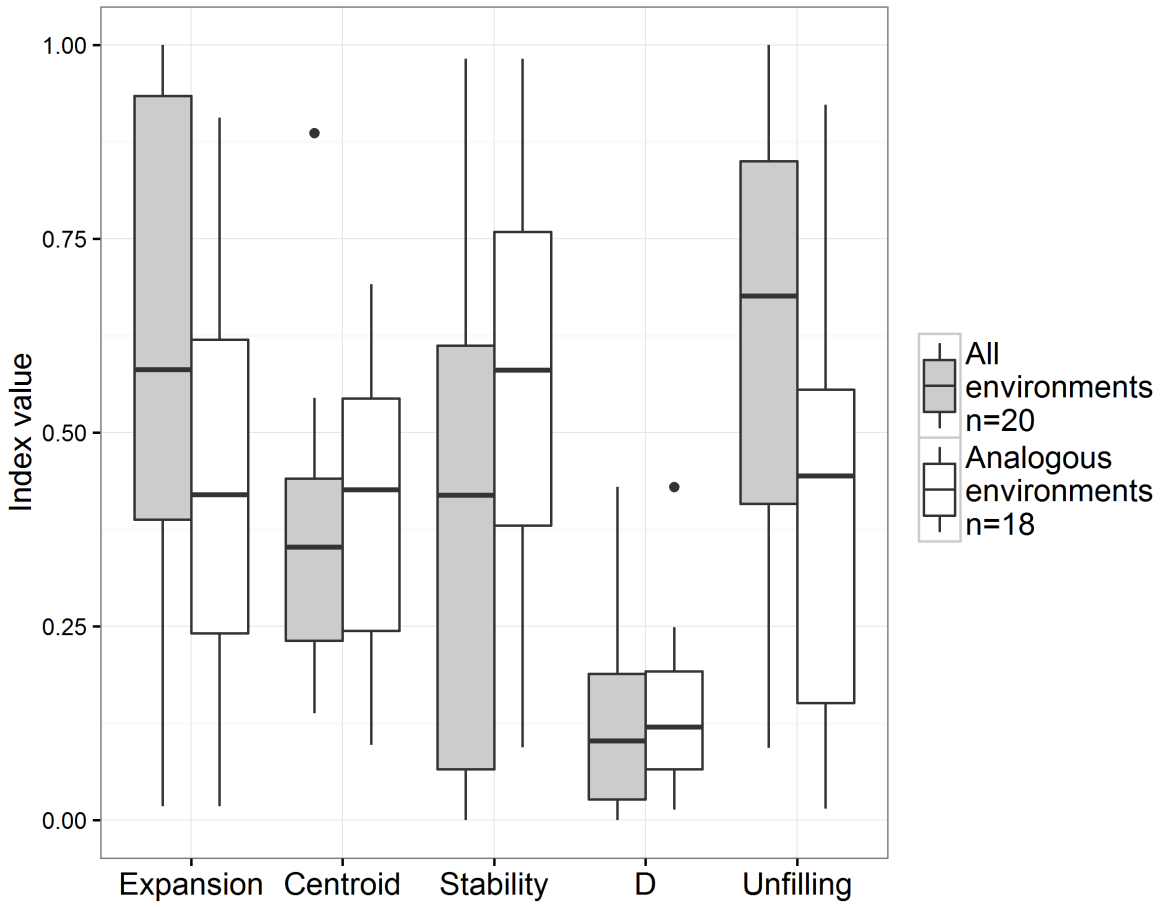


Figure 2.2 Boxplot of the niche metrics computed in all environments (n=20) and analogous environments only (n=18). The bar represents the median value and the upper and lower hinges, the 25th and 75th percentiles respectively. For two species, the metrics in analogous environments were not able to be computed because native and invasive niches were completely in non-analogous environments.

Niches in the native and invaded range differed significantly for all species (niche equivalency test, Table 2.3). However for most the species, invasion patterns were consistent with environmental patterns seen in the native range (niche similarity test, Table 2.3) with the exception of *Eriocheir sinensis* (Milne-Edwards 1854, Varunidae), where the test was rejected.

Table 2.3 Niche equivalency and similarity test results using the D metric. The first symbol indicates statistical significance for the equivalency test and the second symbol for the niche similarity test. Symbols and abbreviations: * (significant at *P*-value < 0.05) and ns (non-significant).

Species name	D metric
Corbicula fluminea (O. F. Müller, 1774)	0.19*ns
Aedes albopictus (Skuse, 1895)	0.43*ns
Orconectes virilis (Hagen, 1870)	0.14*ns
Procambarus clarkii (Girard, 1852)	0.21*ns
Bithynia tentaculata (Linnaeus, 1758)	0.03*ns
Bythotrephes longimanus (Leydig, 1860)	0.02*ns
Cercopagis pengoi (Ostroumov, 1891)	0.03*ns
Cipangopaludina japonica (von Martens, 1861)	0.09*ns
Dreissena polymorpha (Pallas, 1771)	0.08*ns
Dreissena rostriformis bugensis (Andrusov, 1897)	0.01*ns
Eriocheir sinensis (Milne-Edwards, 1854)	0.19**
Gammarus tigrinus (Sexton, 1939)	0.00*ns
Limnoperna fortunei (Dunker, 1857)	0.09*ns
Orconectes limosus (Rafinesque, 1817)	0.13*ns
Pacifastacus leniusculus (Dana, 1852)	0.11*ns
Pomacea canaliculata (Lamarck, 1828)	0.25*ns
Potamopyrgus antipodarum (Gray, 1843)	0.20*ns
Pseudodiaptomus inopinus (Burckhardt, 1913)	0.00*ns
Rhithropanopeus harrisii (Gould, 1841)	0.18*ns
Valvata piscinalis (Muller, 1774)	0.06*ns

Removing marginal climates using different thresholds had a significant effect in niche expansion and unfilling (Friedman rank sum test, p-value < 0.00001) which suggests that for some species, part of their niche is found in marginal climates.

2.3.2 Niche conservatim and SDM performance

Using the Kendall correlation test, the p-value for all the niche metrics was > 0.05 indicating that in this study, there was no evidence that niche conservatism influenced SDM performance (Appendix A.10).

2.3.3 Hotspots of invasion and niche stability in New Zealand

Three species were not included in this analysis because, for two species (*D. villosus* and *H. anomala*), there were insufficient records in the native range and because the third species (*Potamopyrgus. antipodarum*) is native to New Zealand. More than half of New Zealand was found to be climatically

suitable for a number of species (4-11 species) (Figure 2.3). In comparison, more than 25% of New Zealand climates corresponded to areas of climatic niche stability for the same two categories. (Figure 2.3). Interestingly, some hotspots of niche stability overlapped with hotspots of invasion (Figure 2.4). However, in some areas such as Auckland, hotspots of invasion were not identified as hotspots of niche stability.

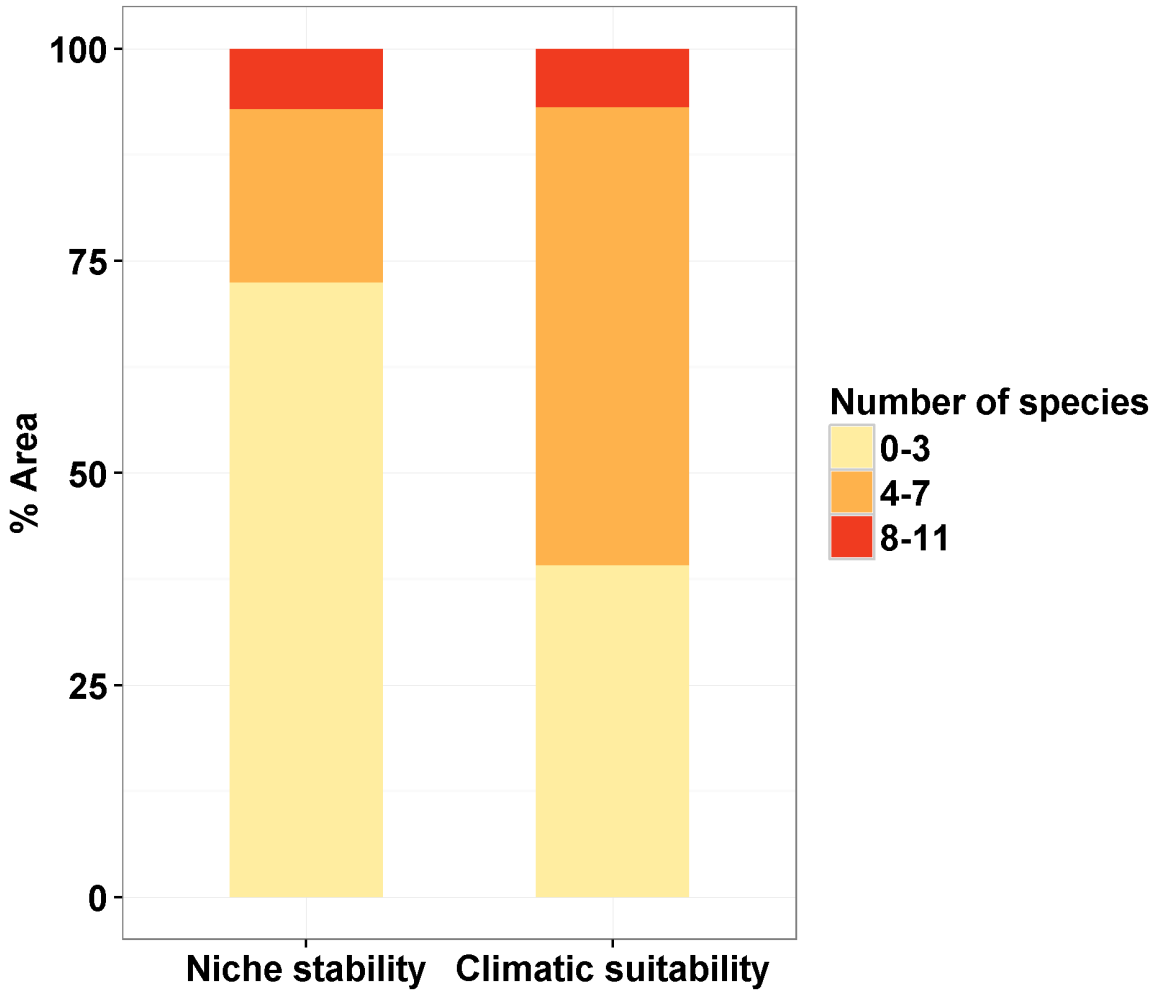


Figure 2.3 The bar diagram indicates the percentage of total area in New Zealand that is climatically suitable and matches niche stability environments for multiple invasive freshwater invertebrates (19 species).

Closer examination of specific biogeographic units, showed at least 9 out of 29 units had more than half their area at risk for at least 2 species (Figure 2.5). The biogeographic units that should be carefully monitored are Auckland, Banks Peninsula, Canterbury, Clutha, northern and western Northland, Otago Peninsula, Taieri and Waitaki.

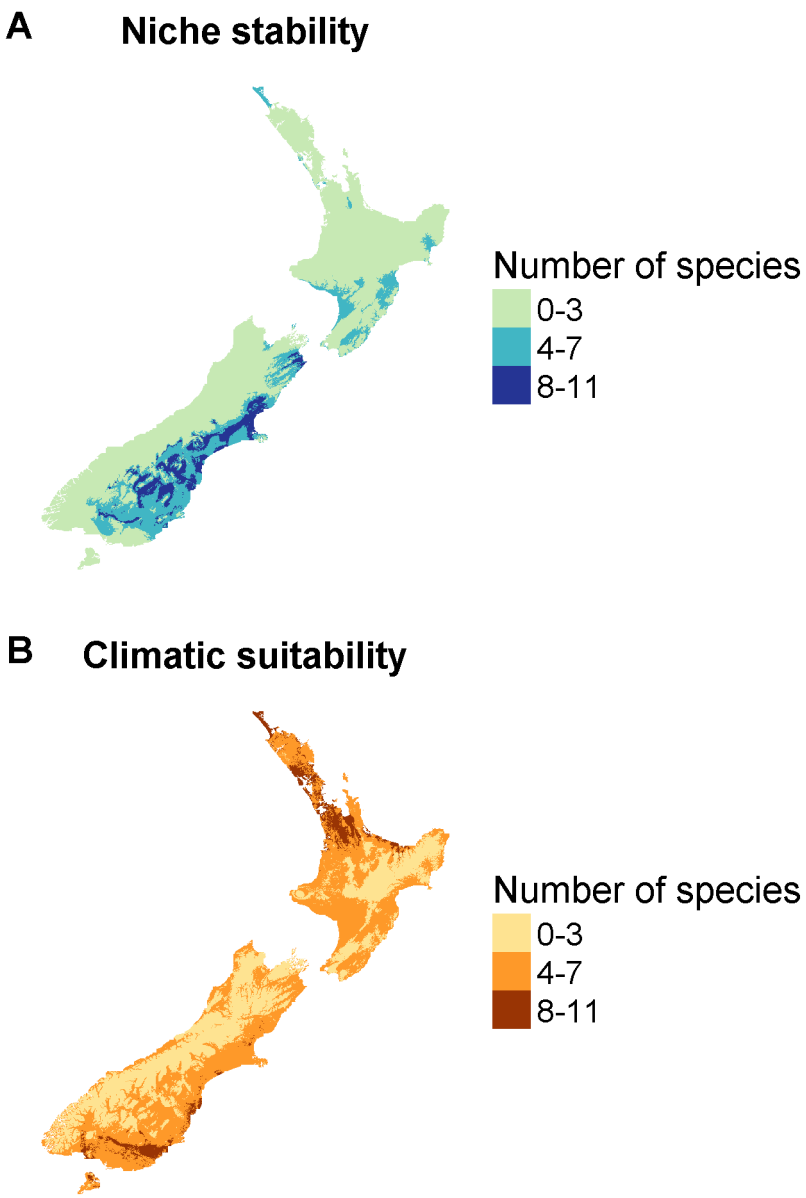


Figure 2.4 (A) Map representing potential hotspots of niche stability (B) potential hotspots of invasion assessed by climatic suitability. See Figure 2.5 for locating the biogeographic units.

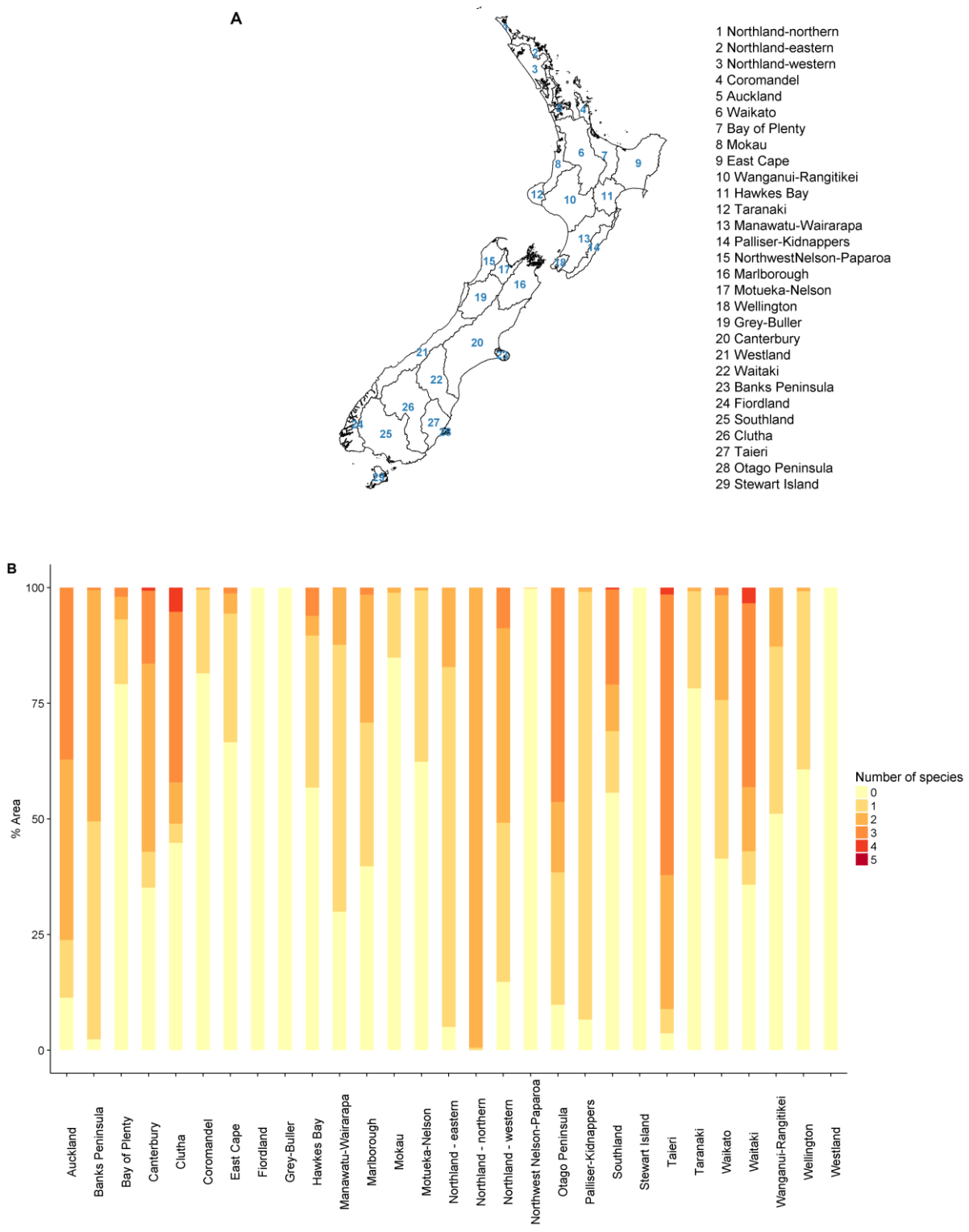


Figure 2.5 (A) Map represents biogeographic units in New Zealand suggested by Leathwick et al. (2007). (B) The bar diagram illustrates the percentage of area by biogeographic unit that is at high risk of invasion by multiple species. High risk of invasion is indicated when locations are climatically suitable and their environments matched niche stability environments.

2.4 Discussion

2.4.1 Niche conservatism

Using several species, this study provided for the first time, an extensive assessment of the frequency of niche conservatism in invasive freshwater invertebrates and attempted to show the potential benefits of niche conservatism in predictions of invasive species distributions. Moreover, using New Zealand as a case study, this research proposed a novel framework to determine areas of high risk of invasion by combining information on niche conservatism and climate suitability.

With respect to the assumption of niche conservatism, the invasive freshwater species studied here did not entirely maintain their native niche characteristics as demonstrated by their niche equivalency results (Table 2.3). Most of the species (90%) showed changes in their niche measured by their centroid and expansion indices (Figure 2.2). Even considering the most conservative results after removing non-analogous climates, more than 80% of the aquatic invertebrates did not retain their native climatic niche in the invaded range. For studies using the same methodology as this study, niche changes seem to be less prevalent for marine fish, birds and plants where 33%, 29% and 14% of the species niche shifted respectively (Petitpierre et al., 2012; Strubbe et al., 2013; Parravicini et al., 2015). The fact that aquatic species appear to show less niche conservatism than other organisms could be due to several reasons. Some niche shifts could be the result of not including other important variables for the species niche. In fact, some studies have already noted that the degree of niche conservatism can change with the variables used, specifically when using “relaxed” variables, in other words, variables that have low or localized impact on species range (Strubbe & Matthysen, 2014). Using birds as a case study, Strubbe & Matthysen (2014) found that niche shifts were less common along precipitation seasonality, which is an important variable in both ranges, compared with to other variables that have a localized impact in only one range. Other non-climatic factors, such freshwater variables and anthropogenic influence clearly need to be investigated (e.g González-Moreno et al., 2014; Gallardo et al., 2015) but separately from macroclimate factors, to assess their relative effect (Guisan et al., 2014). Unfortunately, it remains a challenge to study freshwater species as freshwater variables are usually not available at a global scale, so this area of study is a field for improvement (Loo et al., 2007). On the other hand, the high prevalence of niche unfilling in freshwater organisms might be explained by short introduction times into the invaded range where species did not have enough time to colonize all suitable environments. Indeed, Strubbe et al. (2013) estimated that birds having recent introduction history showed more niche unfilling which reflects the ongoing dispersal in the invaded range. Additionally, for freshwater invertebrates, their particular dispersal strategies may slow down dispersal in their invasive range, potentially resulting in more niche unfilling. With the exception of flying insects, most freshwater species have passive dispersion depending on, for example, wind, drift and other animals, for which they have to

possess specific traits, such as resting stages and specific body adaptations to hitchhike (Bilton et al., 2001; Havel et al., 2015). Therefore, mainly human-assisted dispersal will promote their spread at a large scale, especially for those species lacking the aforementioned characteristics.

In this research, species showed a realized niche expansion in both analogous and non-analogous environments. I also found that some of the niche changes were observed in marginal climates. There is an ongoing debate about the mechanism for niche changes in analogous and non-analogous environments (Guisan et al., 2012; Webber et al., 2012). Indeed, differentiating evolutionary mechanisms from other ecological mechanisms for niche expansion in non-analogous environments is challenging, considering that the species does not have those environments available in its native range. What is clear, is that changes in the fundamental niche cannot be detected with distribution data. Colonization of new environments in the invaded range not occupied in the native range could be the result of the absence of biotic interactions such as enemy release or absence of competition (Catford et al., 2009). For example, in its native range, *Orconectes virilis* (Hagen, 1870, Cambaridae) can be infected by a parasite, *Microphallus spp*. making it more vulnerable to predation (Reisinger et al., 2015). Furthermore, Hill & Lodge (1999) report that *O. virilis* is outcompeted in its native range by another invasive species *O. rusticus*. Similarly, for *Potamopyrgus antipodarum* (Gray 1843, Hydrobiidae), native populations can show a high incidence of parasitic trematodes, whereas in the invasive range their incidence is very low (Alonso & Castro-Díez, 2012). Such examples clearly illustrate that biotic exclusion in the native range could lead to a realized niche expansion in the invaded range. The realized niche may also change when natural dispersal barriers are transgressed. For example, island endemics such as *P. antipodarum* can occupy new environments in the invaded range because of pre-adaptation to those environments (Alexander & Edwards, 2010). However, challenges remain to differentiate between an evolutionary change, phenotypic plasticity and ecological responses (Moran & Alexander, 2014). For instance, C*orbicula fluminea* (Müller 1774, Cyrenidae) and *Dreissena bugensis* (Andrusov 1897, Dreissenidae) both show morphological plasticity in their invaded range, however, whether this response resulted in increased fitness as required to persist in the new area, has not been demonstrated detected yet (Sousa et al., 2007; Peyer et al., 2010). Asian tiger mosquito (*Aedes albopictus*) has been shown by Lounibos et al. (2003) to provide a good example of spread assisted by rapid evolution where its photo-periodically induced diapause has changed in the northern latitudes of the USA in response to early arrival of winter days, and reduced in more southern latitudes to exploit longer days. Likewise multiple invasions of the copepod *Eurytemora affinis* (Poppe 1880, Temoridae) in North America and Asia were followed by an osmoregulatory evolution that allowed the species to shift from native saline habitats to freshwater habitats (Lee, 2015).

2.4.2 Modelling considerations

I found no evidence that niche conservatism could potentially improve the performance of the SDM used in this study. However, other studies have found a positive relationship between SDM performance and niche overlap and conversely a negative relationship with niche change metrics (Petitpierre et al., 2012; Strubbe et al., 2013). Both these studies measured the performance of one range-based SDM, while in the current study, both invasive and native range distributions were used which might explain these contrasting results. Nevertheless, this study shows that assessing niche conservatism can provide useful insights for the use of SDM. The prevalence of niche changes in invasive freshwater species suggests that using one range to predict another is not appropriate for these species thus SDM have to be calibrated using both native and invaded ranges.

2.4.3 Implications for risk assessment, surveillance and management

Detecting niche changes in the realized niche may reveal concealed ecological or evolutionary processes that allow species to colonize new environments. Thus, considering niche dynamics enables species that might challenge surveillance and management to be identified.

The information on niche dynamics could also be used in a invasive species risk assessment. Typically in a risk assessment, the likelihood of a species to enter and establish as well as the biological and economic impacts is evaluated. Several criteria are considered such as the presence of host, environmental characteristics of the area of interest as well as biological factors that makes the species of particular concern (Pearson, 2006). Species indicating high niche expansion could be considered of higher concern as they may hold characteristics that allows them to colonize new environments.

Further examination of where these changes occur may help to determine potential control strategies. For example, analogous environments that are colonized in the introduced range but are not in the native range could indicate the presence of an “enemy” in the native range that could be used for biological control. Only experiments using the populations that showed niche changes will reveal the true mechanism behind this change. For instance, a comprehensive framework such as that provided Rey et al. (2012) and Krehenwinkel et al. (2015), uses species distribution modelling, experimental and genetic approaches were used to shed light on the evolutionary mechanisms behind climatic niche shifts.

Combining hotspots of invasion and niche stability haven’t been explored before. Yet it is a useful way of prioritizing areas for monitoring and surveillance. For instance, in this study, the Auckland area was indicated as high risk as it was shown to be climatically suitable for at least eight invasive species (Figure 2.4). However, that area is not identified as a hotspot of niche stability.

Within the context of prioritization of areas for surveillance and monitoring, the Auckland area could be considered less critical compared with Northland where hotspots of invasion match hotspots of niche stability and thus where the species are more likely to establish.

2.5 Conclusion

This research showed that niche conservatism in invasive freshwater species is the exception rather than the rule, highlighting the challenges for anticipating their impact in freshwater ecosystems. The study showed that New Zealand is generally climatically suitable for many invasive freshwater invertebrates. I identified biogeographic units that are at most risk and used a novel approach to prioritize those areas. In New Zealand, unintentional introductions of high risk species, particularly micro-invertebrates or species having dormant stages such as a diapausing egg, could likely occur through the aquarium trade (Duggan, 2010; Collier et al., 2011) or on recreational equipment, such as fishing and sports gear (Smith & Dodgshun, 2008). Such pathways should be carefully considered along with the identification of suitable areas for establishment and potential hotspots, as highlighted in this study, for more effective prioritization of areas for surveillance and monitoring.

Chapter 3

Disequilibrium of invasive freshwater species and effects of residence time

3.1 Introduction

Invasive species are one of the major threats to biodiversity and can have considerable impact on ecosystems services and natural resources (Sala, 2000; Pejchar & Mooney, 2009). As a result, it is desirable to predict the environments in which invasive species will occur, to effectively prevent and manage their impact. The most widely used tool to make such predictions are species distribution models (SDM) which represent species fundamental and realized niche (Guisan & Zimmermann, 2000). The fundamental niche represents the environments where a species can live and the realized niche the environments where a species can live, disperse and coexist with other species (Soberón & Peterson, 2005). The task of predicting species distributions is continuously challenged by the fact that invasions are dynamic across space and time. For example, some habitats vary spatially where certain features, such as availability of resources, can make them more or less susceptible to invasions than others (Richardson & Pyšek, 2006; Simberloff, 2013). Similarly, the process of invasion can change through time (Dietz & Edwards, 2006) because stochastic factors such as residence time for a species that has been accidentally introduced, will determine the likelihood of an invasion. The phenomenon of lag times has also been recognized to affect invasions which involve a long period of inactivity or slow range expansion, often followed by drastic changes of dynamics (Crooks, 2005; Hyndman et al., 2015). Residence time is therefore going to determine the likelihood of species reaching equilibrium in the introduced range, in other words, when a species occupies all climatically suitable habitats and is absent from all unsuitable habitats (Araújo & Pearson, 2005).

Non-equilibrium of an invasive species' distribution can have major repercussions for the management of that species. First, non-equilibrium can cause species distribution models to underestimate the species' potential distribution. This underestimation is likely to be particularly severe in the early stages of invasions where only a small part of the species niche is observed (Guisan & Thuiller, 2005; González-Moreno et al., 2014). For example, in a study of the spread of the invasive forest pathogen, *Phytophthora ramorum*, Václavík & Meentemeyer (2012) found SDM developed during the early stages of invasion tend to underestimate the potential distribution of the species compared to models developed closer to equilibrium. Second, the dynamics of the species' distribution as it moves towards equilibrium can shed light on the stage of invasion. For instance,

identifying whether the invasion process is in a lag phase will indicate opportunities to effectively manage an invasive species (Welk, 2004).

There is considerable evidence showing that most species, even non-invasive ones, are not in equilibrium with their environment because that requires unlimited dispersal to suitable areas and high rates of extinction in unsuitable areas (Araújo & Pearson, 2005; De Marco et al., 2008), or, long time periods for a species to equilibrate. However, what is not yet clear is when, and at which rate, species can reach equilibrium. Few studies (e.g Pyšek & Prach, 1995; Williamson et al., 2009) have quantified the progress to equilibrium for invasive species and most focused on plants making it hard to generalise to other taxa. Moreover, the studies measured 'range equilibrium', in other words, measuring whether species have filled their potential geographic space (Bradley et al., 2015). For example, Pyšek & Prach (1995) studied the rate at which the invasive *Impatiens glandulifera* spread in the Czech Republic and determined the year when the species would reach its range equilibrium using the number of localities occupied across time. Similarly, Williamson et al. (2009) assessed when range equilibrium would be reached for invasive and native higher plants in four areas in Europe using their change in distribution over time. However, a range disequilibrium does not necessarily mean that the species hasn't reached its climatic equilibrium, if it has fully filled its climatic space (Bradley et al., 2015). This relates back to Hutchinson's biotope-niche duality framework, which postulates that a one-to-one correspondence between niche space and the biotope (geographic space) does not exist. In other words, one point in the niche space can correspond to many points in the biotope (Colwell & Rangel, 2009). Therefore, describing a climatic equilibrium will be more informative than a range equilibrium in the context of validating the use of SDM. Two types of climatic disequilibrium can be detected in the invaded range (Figure 3.1), 1) when the species does not occupy all climates occupied in the native range (realized native disequilibrium), or, 2) when the species does not occupy all climates from other parts of the potential niche, not previously occupied in the native range (potential niche disequilibrium). The potential niche is the intersection between the fundamental niche and the available climates in the geographic space (Soberón & Nakamura, 2009). In the native range, the entire potential niche is not necessarily filled due to dispersal or biotic restrictions. However in the invasive range, it is expected that as residence time increases, climates previously occupied, and those climates excluded by biotic interactions and/or dispersal restrictions in the native range, will progressively be filled (Gallagher et al., 2010; Li et al., 2014).

In this research, I aimed to contribute to the discussion of species equilibrium by providing, for the first time, an evaluation of niche dynamics and the time needed for a number of selected invasive freshwater invertebrates to reach climatic equilibrium. This research specifically aimed to answer the following questions: do invasive species approach equilibrium as residence time increases? How far are they from equilibrium?

The realized climatic niche of nine invasive freshwater species was characterized using their global occurrence data. The climatic disequilibrium in the invasive range was measured by looking at differences between native and invasive niche across time. The two types of disequilibrium can be measured by looking at two parts of the realized niche in the invasive range (Petitpierre et al., 2012): niche unfilling which are the environments that the species occupies only in its native range (realized native disequilibrium), and, niche expansion, which are the new environments not previously occupied in the native range (potential niche disequilibrium) (Figure 3.1). I hypothesised that climates analogous to the native niche will be progressively occupied in the invaded range, thus niche unfilling should decrease as residence time increases (Figure 3.1). In addition, occupation of new climates, not previously occupied within the native range, should increase with time thus niche expansion should increase with time.

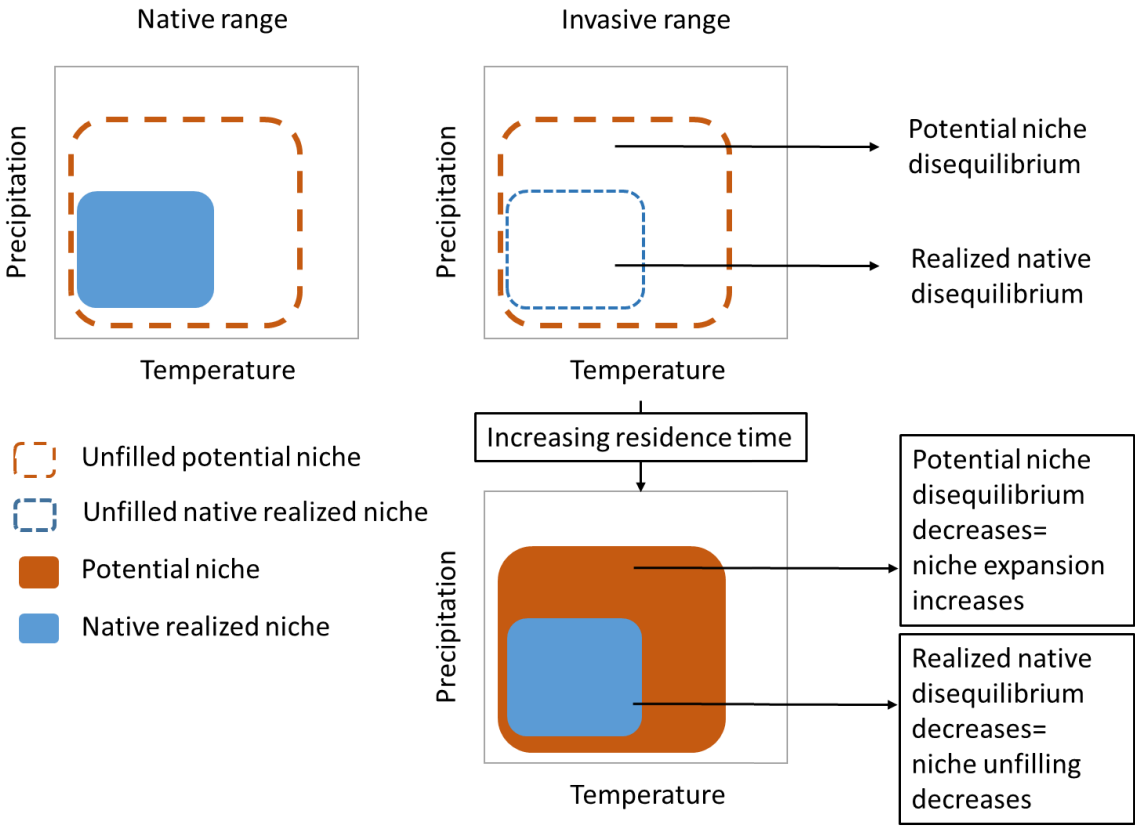


Figure 3.1 Schematic illustration of species niche in two hypothetical environmental gradients and hypotheses tested in this study. In the invaded range, I expect that as residence time increases, species will occupy environments analogous to the native niche, therefore realized native disequilibrium should decrease. I also expect that as residence time increases, species will occupy new environments not previously occupied in the native range, therefore potential niche disequilibrium should decrease. Note that in the native range potential niche is not necessarily fully filled because of biotic or dispersal restrictions.

3.2 Methods

3.2.1 Species occurrences and environmental variables

Nine of the species described in Chapter 2 (Table 2.1) that had broad temporal coverage of their distribution (at least 30 occurrence points) (Figure 3.2), were selected for this study. The species were Gammarus *tigrinus* (Sexton, 1939), *Rhithropanopeus harrisii* (Gould, 1841), *Bithynia tentaculata* (Linnaeus, 1758), *Pomacea canaliculata* (Lamarck, 1828), *Cipangopaludina japonica* (von Martens, 1861, *Orconectes limosus* (Hagen, 1870), *Bythotrephes longimanus* (Leydig, 1860), *Dreissena polymorpha* (Pallas, 1771) and *Potamopyrgus antipodarum* (Gray, 1843). Additional occurrence locations were obtained for *Potamopyrgus antipodarum* from Booker et al. (2015). For each species' dataset, only one occurrence point per grid cell of resolution 10 arc minute (0.17°) was used to minimise spatial autocorrelation (Veloz, 2009; Kramer-Schadt et al., 2013).

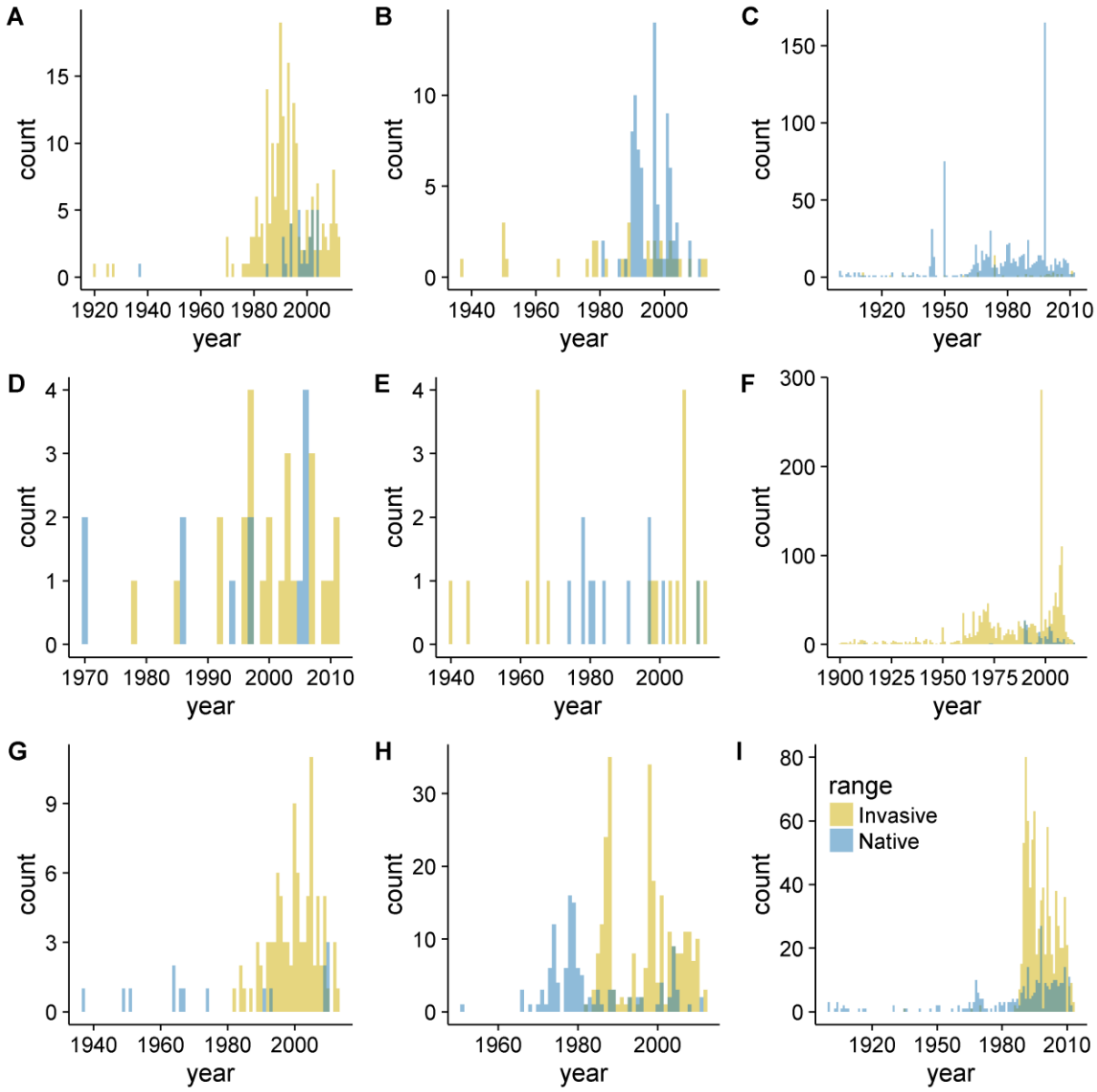


Figure 3.2 Number of occurrences per year by range for: a) *Gammarus tigrinus,* b) *Rhithropanopeus harrisii,* c) *Bithynia tentaculata*, d) *Pomacea canaliculata,* e) *Cipangopaludina japonica,* f) *Orconectes limosus,* g) *Bythotrephes longimanus,* h) *Dreissena polymorpha* and i) *Potamopyrgus antipodarum.*

The climatic characteristics for the occurrence points and the geographic background (available climates for the species) were extracted from the Climond database (Kriticos et al., 2012). Because the data reflect the average, extreme and the seasonality of hydrothermal conditions, the environmental variables chosen to characterize species' niche and geographic background were temperature, solar radiation and precipitation (Table 2.2). The Climond database contains 30-year climate data monthly averages from 1960-1990. Note, however, that some of the species invasions studied took place over sometimes a different (and longer) time period than Climond. In some cases, the time period ranged from 1900 to 2014. However, the range of climate fluctuations over that period is small in comparison to the range of climates spatially occupied by the species. For example,

the global average temperature has increased 0.8°C from the beginning of the 20th Century to beginning 21st Century (Hansen et al., 2010) whereas the minimum average range of temperature occupied by the species is close to 9°C. Therefore, the bias involved with mismatching occurrence and the timeframe of the climate data will be small.

3.2.2 Quantifying climatic disequilibrium across time

The climatic disequilibrium in the invaded range was characterized by quantifying the differences between the invasive and the current native niche (based on the accumulated temporal information). These differences were characterized using a principal component analysis (PCA) where the occurrence and geographic background points were smoothed by applying a kernel function as described in detail in Chapter 2 (Broennimann et al., 2012; Petitpierre et al., 2012). This framework was shown by Broennimann et al. (2012) to be the most accurate for quantifying differences between niches.

Because the aim of this study was to determine the full extent of the realized niche in the invaded range, it was necessary to accumulate information from environments occupied by the species over time. Thus, an assumption was made that once a species occupied a location, it will remain there over the consecutive time steps. Only years where at least five locations were available for both invasive and native niches were used for the analysis as recommended by Broennimann et al. (2012).

The geographic background was delimited using freshwater ecoregions that overlapped with the current species distribution. I used the freshwater ecoregions delimited by Abell et al. (2008). For example for *P. antipodarum,* the current distribution overlapped with 31 freshwater ecoregions which were selected to represent the geographic background for the species. The principal component axes were first constructed using the geographic background. The environments occupied by the species were projected subsequently along the components. This was done to prevent an effect of the repeated environments occupied by the species (due to accumulated temporal data) in the construction of the components. At each year, low occurrence density values were removed using the 95th quantile from the last year in the whole sequence of time points. This conservative threshold was used because, in some cases, species occurrences were scattered in the environmental space and by applying a kernel smoother the occurrence densities went beyond the limits of the geographic background.

The two niche indices, unfilling and expansion, were computed at each year only for environments available in both the native and invasive range (analogous environments) (Petitpierre et al., 2012). As explained in detail in Chapter 2, unfilling represents the environments occupied in

the native range (realized native disequilibrium). Expansion represents new environments occupied in the invaded range that are not in the native range (potential niche disequilibrium). A decrease of the unfilling metric (from 1 to 0) across time indicates that the species is occupying environments in the invasive range that resemble the native environment. In other words, species become closer to equilibrium in relation to the native range. On the other hand, an increase of the expansion metric (from 0 to 1) across time indicates that the species continues to occupy new environments in the invaded range not previously occupied in the native range. Here, they are filling part of the niche that was not realized in the native range and thus, they become closer to equilibrium in relation to the potential niche.

To determine if there was an overall change in environments occupied in the invaded range across time, unfilling and expansion were compared between the initial and final time step using a paired Wilcoxon Rank Sum test (R package exactRankTests (Torsten & Kurt, 2015)). A one tail test for each metric was used because it was hypothesized that there would be a decrease in unfilling and increase of expansion as discussed previously.

3.2.3 Time to equilibrium in the invaded range

A species would reach a realized native equilibrium when all the climates occupied in the native range that are also available in the invaded range, become occupied, which is when the unfilling metric becomes 0. To evaluate when a species would reach potential niche equilibrium, it would require information on the whole potential niche which is not available in this study and thus was not considered here.

The number of years from the first record used in the niche analysis until niche unfilling becomes 0 was predicted using a generalized least squared regression (GLS) between niche unfilling and time (Zuur et al., 2009a). A regression was performed only for species having at least ten measures of unfilling metric across time. Since the environments occupied at time *t* will depend on the environments occupied at time *t-1*, the assumption of independence in the residuals is violated. If observations are correlated, the true sample becomes smaller, affecting the degrees of freedom of the regression. This in turn will affect the significance of the regression coefficients where the *P* value and confidence interval will be smaller than they should be (Mcgill, 2012). The lack of independence in the residuals can be dealt with by incorporating a temporal correlation structure between residuals in the regression, which can be achieved using a generalized least squared regression (GLS) (Zuur et al., 2009a). Several linear models were tested with and without a residual autocorrelation structure using different autocorrelation functions as suggested by Zuur et al. (2009b). These autocorrelation structures also known as ARMA error structures, have two parameters: p, which determines the number of autoregressive parameters and q, which determines the number of

moving average parameters. I tried a combination of parameters p = {1, 2} and q = {0, 1, 2, 3} and used AICc (corrected Akaike's Information Criterion) as selection criteria to determine the best combination. The AICc metric is an alternative to AIC when the sample size is small compared with the number of parameters estimated (Burgman & Anderson, 2002). The model that showed improvement in terms of AICc compared to the model without autocorrelation structure, and that showed the least complex ARMA structure, was selected (Zuur et al., 2009b). The unfilling index is a proportion, and, therefore, required a transformation to approximate the linear modelling assumptions. Warton & Hui, Francis K. (2011) recommended the logit transformation because transformed regression coefficients are easy to interpret and results in sensible predicted values, which can be easily transformed back to the original scale. The logit transformation is also in agreement with empirical evidence of a sigmoidal pattern of spread where the rate of invasion slows down as the number of suitable habitats decreases (Perrins et al., 1993; Pyšek & Prach, 1995). One challenge of the logit transformation, however, is that when transforming values equal to 0 and 1, they become undefined and approach $-\infty$ and$+\infty$ respectively. As recommended by Warton & Hui, Francis K. (2011), a small value ε was added to both numerator and denominator of the logit function, which would result in minimal bias. In the current study, ε was computed as the minimum non-zero value of 1- y, where y was the proportion (Warton & Hui, Francis K., 2011). Model predictive power was assessed by calculating the Pearson correlation measure to its square (pseudo-R-squared), between the observed data and the predicted data (Zheng & Agresti, 2000).

In order to determine the total time required for a species to reach realized native equilibrium in the invaded range, the species introduction date in each continent was determined from the literature. The median year of introduction was calculated for each species using the introduction year from all invaded continents present in the dataset. Analyses were carried out using R (R Core Team, 2015) with packages nlme for implementing GLS regression (Pinheiro et al., 2013) and MuMIn for computing AICc (Bartoń, 2016).

3.3 Results

3.3.1 Climatic disequilibrium and niche dynamics across time

Niche indices were computed over a shorter timeframe than encompassed by the available data to ensure that at least five points from both the invasive and native range were used as recommended by Broennimann et al. (2012). The number of years between the first and last time step, for which niche indices were computed, differed for each species and ranged from 9 to 77 years. Species showed a significant decrease in niche unfilling between the first and last time step (Wilcoxon rank sum test, p-value = 0.02), however, there was no evidence for a significant increase in niche expansion between the first and last time step (p-value = 0.89) (Figure 3.3). In the last time step, the

degree of unfilling varied among the nine species. Some species did not fill very much of their niche in the invaded range in relation to the realized native niche (unfilling close to 1), compared with others that had filled up to 85% (unfilling = 0.15). All species expanded into new environments, but the extent of the expansion was variable. The expansion varied from at least 46% (expansion = 0.46) of the niche into new environments to an expansion of 1. Such species colonized only new environments compared to the native range. From the earliest record for each species available in the dataset, all showed a high degree of expansion (from 0.44 to 1) (Figure 3.3). These results suggest that, at the earlier stages of invasion, the species were able to occupy climates that were different from their native habitats.

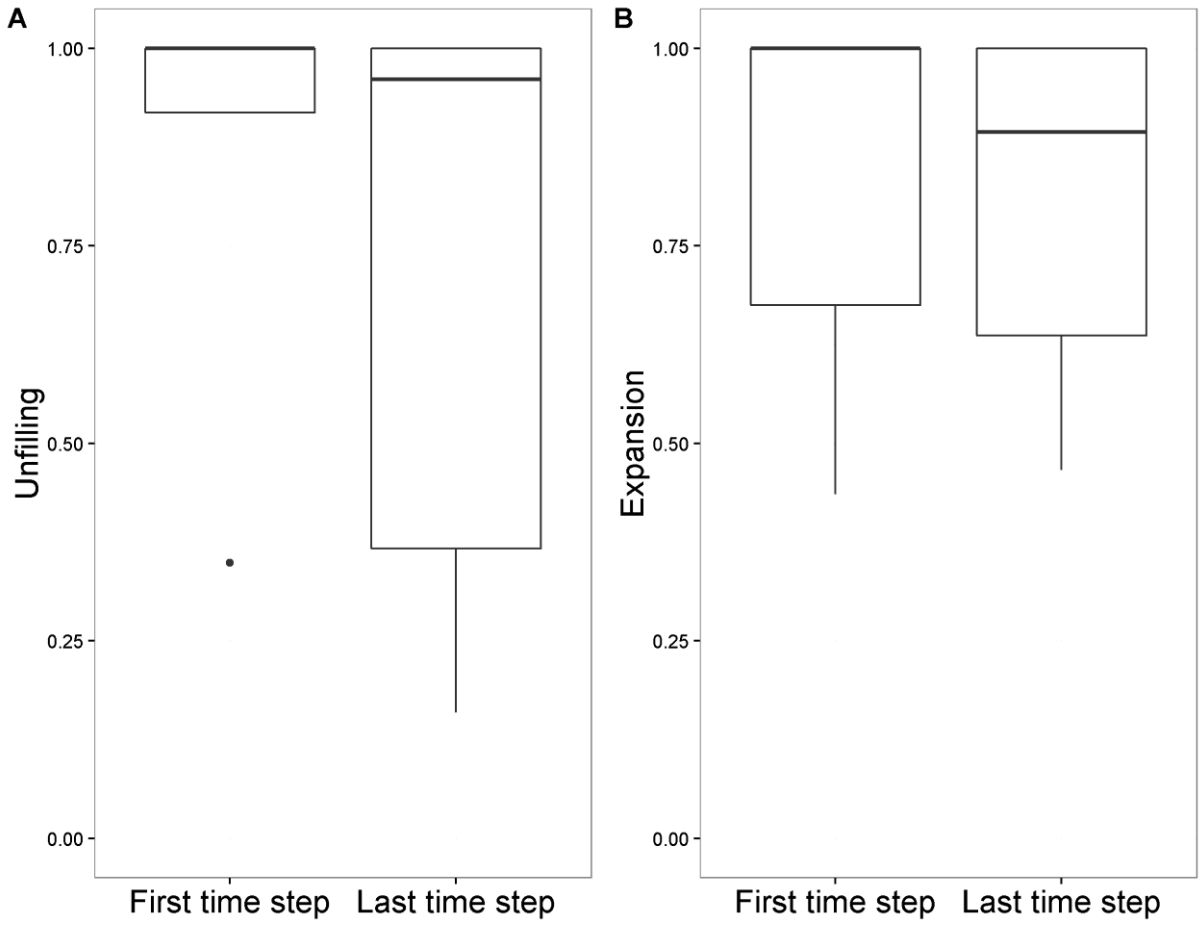


Figure 3.3 Boxplot of niche unfilling (A) and niche expansion (B) for the first and last time step.

3.3.2 Time to equilibrium in the invaded range

I attempted to predict the number of years that each species would need to reach a realized native equilibrium in the invaded range (Figure 3.4). Regressions were done for six out of the nine species because they had at least ten measures of niche unfilling across time. All models for each species indicated temporal autocorrelation. As a result the ARMA parameters for the final model can be found in Table 3.1. The regression coefficients show that time was significant for five species (Table 3.1); however, it did not explain the change in niche unfilling for *Dreissena polymorpha.* If the

processes driving the invasion continue as they are from the first time step, *Potamopyrgus antipodarum* would fill its niche in about 100 years (Figure 3.4), *Rhithropanopeus harrisii* in about 70 years, *Pomacea caniculata* in 14 years and finally, *Bythotrephes longimanus* was predicted to reach equilibrium in 118 years. *Bithynia tentaculata* appears to be filling its niche much slower, potentially going through a lag phase as it will require much more than 120 years to fill its niche in the invasive range.

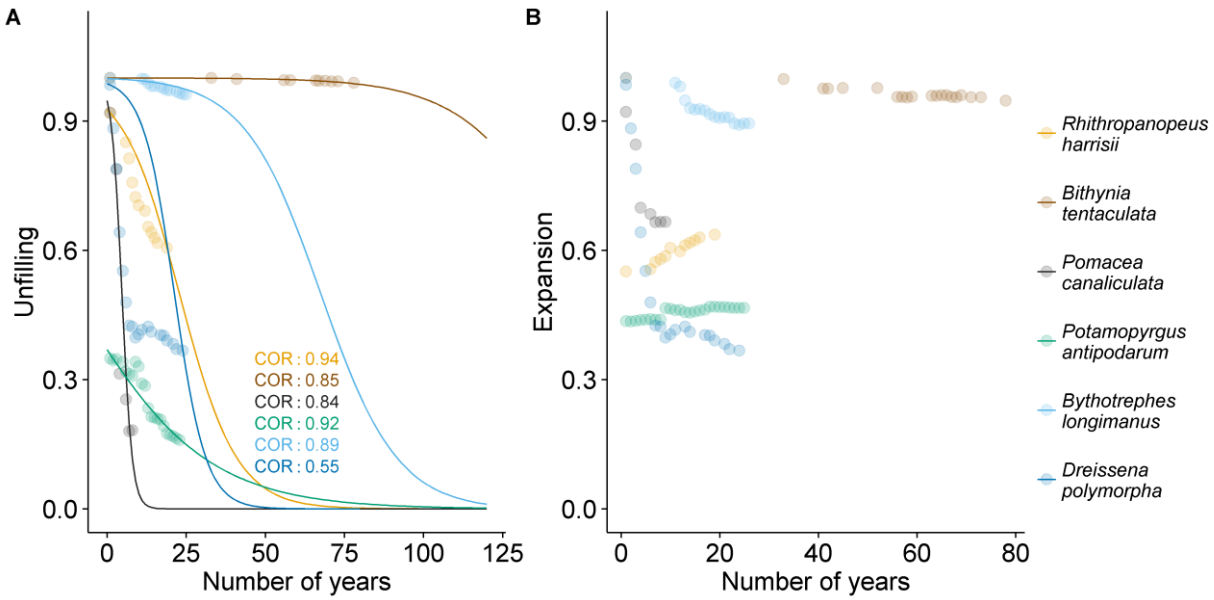


Figure 3.4 Niche dynamics of species across time (A) niche unfilling and (B) niche expansion. Points represent unique measures available across time and lines represent predictions using GLS regression.

With respect to the median year of first introduction across the invasive ranges, *Potamopyrgus antipodarum* would require in total, 195 years to reach realized native equilibrium, *Rhithropanopeus harrisii* around 154 years, *Pomacea canaliculata* only 21 years, and finally, *Bythotrephes longimanus* would require 120 years (Table 3.2). Thus the average time to realized native equilibrium for these invasive freshwater invertebrates is 122 years (± 74). Time to equilibrium using the expansion index cannot be predicted because information on the potential niche is required and this was outside of the scope of this study.

Table 3.1 Regression coefficients from the logit transformed data and parameters for the autoregressive moving average correlation structure for the best model according to AICc criteria. The letters p and q represent the order of the autoregressive process and the order of the moving-average process respectively. Bold parameters highlight significance at threshold 0.05.

	Intercept	Slope	p	q
Rhithropanopeus harrisii	2.53	**-0.11**	1	0
Bithynia tentaculata	**8.91**	**-0.05**	0	0
Pomacea canaliculata	**2.90**	**-0.62**	1	2
Potamopyrgus antipodarum	**-0.53**	**-0.05**	1	0
Bythotrephes longimanus	**5.58**	**-0.08**	1	1
Dreissena polymorpha	4.29	-0.20	1	0

Table 3.2 Median year of introduction across the ranges available in the database and number of years to realized native equilibrium.

Species	Median first year of introduction and standard deviation	Reference for year of introduction	Total number of years to equilibrium
Rhithropanopeus harrisii	1906 ±45	Boyle, Jr. et al. (2010)	154
Bithynia tentaculata	1871	Mills et al., (1993)	lag phase
Pomacea canaliculata	1990±10	Litsinger et al. (2013)	21
Potamopyrgus antipodarum	1895±54	Alonso (2013)	195
Bythotrephes longimanus	1984	Liebig et al. (2016)	120
Dreissena polymorpha	1988	Mills et al. (1993)	Not relevant

3.4 Discussion

This study characterized the degree of disequilibrium of invasive freshwater invertebrates in the invaded range and, from that determined the number of years necessary for species to reach climatic equilibrium in relation to their native niche. The novelty of this study was to use a framework that allows the inclusion of climatic information which describes more accurately the disequilibrium of species distributions.

3.4.1 Climatic disequilibrium

Niche dynamics of invasive species have been rarely studied across time. In this study I have shown by using two niche metrics, that for the species studied here, their climatic niche can change

significantly across time. This research confirms the hypothesis that for the invasive species studied here, many are not at equilibrium with their environment and that they can continue to spread to new environments over time. Consistent with this observation, many studies provide evidence that invasive species are not in climatic equilibrium and time has been described as a factor of primary importance in range filling. For example, in a study of geographic ranges, Bradley et al. (2015) used the distribution of 755 invasive plants and showed that they do not occupy their full potential distribution, and, in general, they tend to be in higher disequilibrium than native plants. Additionally, several studies observed non-equilibrium distributions for even non-invasive species such as vascular plants, breeding birds, reptiles, amphibians and mammals (Svenning & Skov, 2004; Araújo & Pearson, 2005; Munguía et al., 2008, 2012). Several studies have identified residence time as the principal factor explaining range size in plants (Wilson et al., 2007) and marine invertebrates (Byers et al., 2015), as well niche expansion in amphibians and reptiles (Li et al., 2014). However, in this study, we did not find that the degree of niche expansion necessarily increased with time. For example, *B. longimanus*, *P caniculata* and *D. polymorpha* show a clear decrease of expansion over time (Figure 3.4). Decreasing niche expansion indicates that invasion starts at dissimilar environments from the native range followed by a tendency to progress towards stability (Chapter 2), occupying environments similar to the native range. Moreover, in this study, time did not explain the change in realized native disequilibrium for some species. For example, for *Dreissena polymorpha*, time was not significant explaining changes of niche unfilling. The model used did not adequately predict the observed data (Figure 3.4). This finding suggests that another model could be implemented, such as an exponential function instead of a logit function, and that care should be taken to consider assumptions with respect to the rate of niche unfilling. Despite this, time, in general, can and should be used as a predictor of equilibrium because it integrates propagule pressure and other processes that are hard to measure (Richardson & Pyšek, 2006; Byers et al., 2015).

As expected, each species had a different rate of niche unfilling and, when the median year of introduction was considered, the number of years required to reach equilibrium in the invaded range differed among species. There is some empirical evidence that certain species' traits, such as dispersal capability, can affect the likelihood of reaching equilibrium. For example, Araújo & Pearson (2005) showed that in noninvasive species, breeding birds and vascular plants were closer to equilibrium than reptiles and amphibians, which are known to be poor dispersers. Similarly, Munguía et al. (2008) showed that bats were closer to equilibrium than other, typically less mobile mammals. Such studies suggest that dispersal capabilities could play a role in species reaching equilibrium. For freshwater systems, habitat persistence, in theory, should affect species' dispersal abilities, where species from less-stable habitats should exhibit higher dispersal abilities (Ribera & Vogler, 2000). Several studies have shown that lentic invertebrates, which are species associated with less

permanent habitats, such as ponds or small lakes, are closer to equilibrium than lotic species, which dwell in running water bodies (Hof et al., 2012; Sánchez-Fernández et al., 2012). These observations could explain the rapid spread of the golden apple snail as this species is usually associated with less permanent habitats such as ponds and ditches (Cowie & Hayes, 2012). Moreover, range filling in plants has been shown to differ when measured in different countries (Williamson et al., 2009) or different habitats (Pyšek & Prach, 1995), suggesting that invasion history and local communities influence the invasion process. Interestingly, in this study, species that have been introduced more recently seem to have spread faster (Figure 3.5). While there are not enough examples to formalize this trend, it would be interesting for future research to explore this observation in association with human activities and habitat vulnerability.

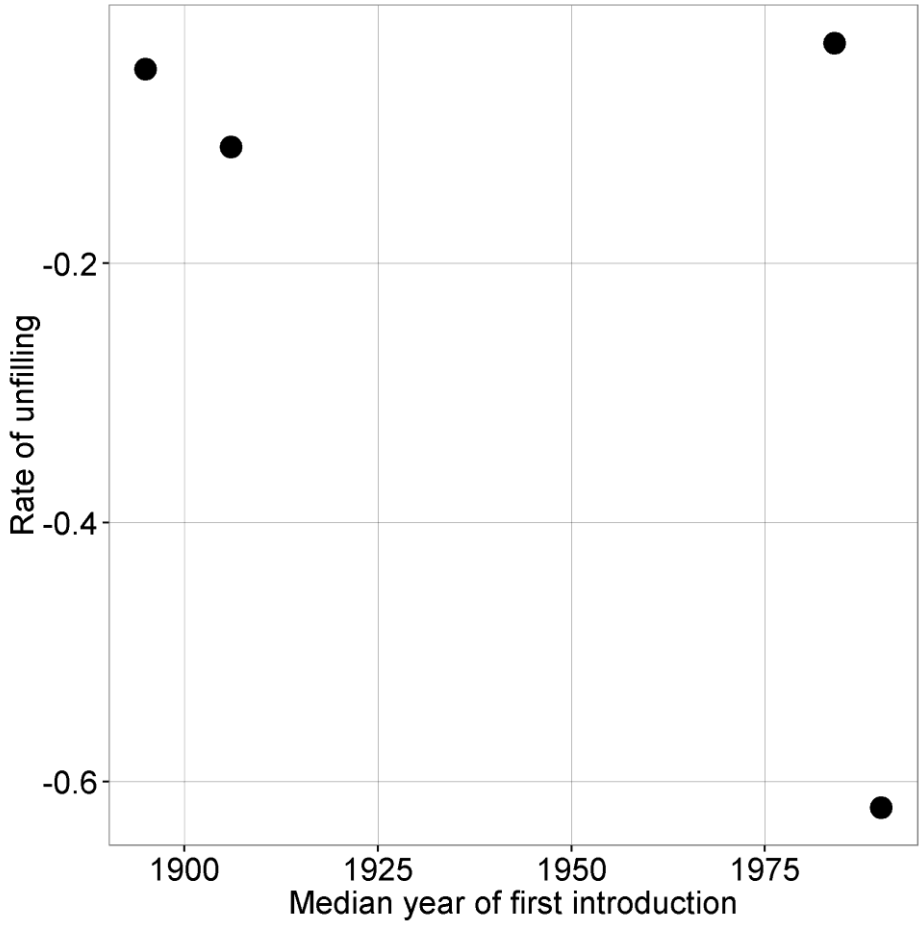


Figure 3.5 Rate of niche unfilling and median year of first introduction. Note that a smaller rate of unfilling implies fast niche filling in the invaded range. Only species with significant regression slopes are shown in this figure.

Welk (2004) suggested that the average time to equilibrium may indicate the necessary time for reliable predictions of the distribution of the species. In this study, for five freshwater invertebrate species, the time to equilibrium ranged from 21 years to 195 years, with an average of

122 years. Despite the small sample size, it seems that invasive freshwater invertebrates required, on average, less time to reach equilibrium in comparison to plants where Williamson et al., (2009), using the distributions of up to 1635 invasive species in four invasive ranges, predicted an average of 150 years to equilibrium. Williamson et al. (2009) stressed an urgent need to identify rapid spreaders. In this study, *Pomacea caniculata* can be identified as fast a spreader and, therefore, should be carefully monitored. Correspondingly, identifying species that appear to be in a lag phase or slow spreaders, like *Bithynia tentaculata* probably provides the best opportunity to control potential impact efficiently. During a lag phase or slow spread, such species do not occupy large areas and their abundance is likely to be low (Welk, 2004).

For the species used in this study, from the first time they were recorded as present in the data set, most showed high niche expansion, indicating that the earlier records were quite different environmentally from those occupied in the native range. Such a result has been previously described by Broennimann et al. (2014), who found the European invasive plant, *Centaurea stoebe,* first colonized environments dissimilar, as well as similar, to the native range. More interestingly, the spread of *C. stoebe* seemed to be faster when it colonized similar environments to its native range and indicated a lag period when the arrival occurred in dissimilar environments. In the current study, the location of the oldest records of invasion suggests that models created at the early stage of invasion may not accurately predict the potential distribution of the species if they are created using only native range information. However, if species spread more slowly within dissimilar environments from the native range, such as indicated by *Centaurea stoebe,* then management might be better facilitated. Further work is required to establish whether this hypothesis holds.

3.4.2 Methodological considerations

One key question about species niche dynamics is how far they are from equilibrium. To my knowledge, few studies have addressed this question (e.g., Pyšek & Prach, 1995; Williamson et al., 2009). I used a framework based on recently developed metrics that enable the estimation of the time necessary to reach climatic equilibrium. It is important to note that the number of years were estimated based on the assumption that the species can disperse to all suitable environments and that biotic interactions will not influence their establishment in the invaded range. Clearly, this is an assumption that will not hold for all species. Thus, potential negative biotic interactions or limits to dispersal are likely to stop species establishment earlier than estimated in this study. Another point to consider is that the niche unfilling metric describes only one type of equilibrium (Figure 3.1) as it is computed in relation to the native range where species distribution can be limited by dispersal restrictions or biotic interactions. The equilibrium in relation to the potential niche was characterized by the niche expansion metric, however, time to full equilibrium cannot be measured for two

reasons. First, the niche expansion index measures the proportion of invasive niche not overlapping with the native niche. Thus it will always be constrained from 0 to 1, regardless of the increase in environments colonized in the invaded range over time. Secondly, predicting the time that the species will reach potential niche equilibrium would require full knowledge of the potential niche.

This study also highlights the need to rigorously record long term data. Occurrence data with temporal information is rather rare, particularly at the initial stages of invasion. It is therefore important to bear in mind that in this study, there might be a bias in the estimation of the temporal niche dynamics. However, the framework used to characterize species niche is designed to reduce this bias by using the kernel smoother function to smooth gaps due to sample bias (Guisan et al., 2014).

3.5 Conclusion

The findings of this research confirm the importance of residence time in the invasion process. Also, the study of temporal niche dynamics helped to identify fast spreaders that should be carefully monitored as well as species going through lag phases. This will indicate the best opportunity to control their impact. By comparing early stages of invasion to their native niche, it was established that species can invade new environments not previously occupied and thus their surveillance and management will be challenged if only information from the native range is available.

Chapter 4

Is extrapolation more uncertain than interpolation when predicting species distribution?

4.1 Introduction

Species distribution models (SDM) have provided useful information for decision making about disease outbreaks management such as ebola in Africa (Pigott et al., 2014), conservation planning, managing invasive species (Guisan et al., 2013) and assessing the response of species to climate change (e.g Thuiller et al., 2005). The most common approach is correlative SDM that relate occurrence information with environmental variables, representing the set of environmental conditions in which a species can survive and persist, the species' realized niche (Hutchinson, 1957; Guisan & Zimmermann, 2000). However, the information used, and decisions made, during the modelling procedure always involves uncertainty. By studying multiple species and even using virtual species, several authors have tested the effect of multiple sources of uncertainty in species distribution modelling, such as the datasets (occurrence and climate records) and the SDM used, as well as variable collinearity. For the studies focused on climate change, the effect of using different general circulation models and emissions scenarios on predictions has also been tested. A common finding among these studies is that the SDM used is the factor contributing the most to uncertainty (Diniz-Filho et al., 2009; Buisson et al., 2010; Thibaud et al., 2014; Watling et al., 2015). Moreover, high uncertainty has been reported especially when SDM are used to predict into unsampled regions (Peterson et al., 2007; Heikkinen et al., 2012; Huang & Frimpong, 2016) or to different times (Dobrowski et al., 2011; Smith et al., 2013; Huang et al., 2016). This problem, also known as 'model transferability', has been one of the biggest challenges for those wishing to use SDM to make decisions and predictions about species potential for establishment in new regions and/or different times.

Reasons for models failing to transfer are often due to a change of species-environment relationship, biotic interactions or genetics and phenotypic plasticity in other regions/times (Randin et al., 2006; Godsoe et al., 2015; Mainali et al., 2015). Model transferability can be also challenged by the degree to which each species niche is known. If predictions are made in novel environmental conditions from what the species is currently known to occupy, requires SDM to extrapolate the species niche. Using correlative SDM to extrapolate species environment relationships into novel environments can be problematic because there is usually no knowledge about the species detailed biological response to those conditions (Fitzpatrick & Hargrove, 2009; Owens et al., 2013). Moreover,

predictions beyond the parameter space from which any model is calibrated are uncertain because of the lack of information to fully validate the models (Elith & Graham, 2009; Owens et al., 2013). Hence, a recommended practice is to report the locations where models extrapolate to highlight uncertain predictions (Fitzpatrick & Hargrove, 2009; Elith et al., 2010; Godsoe, 2012; Owens et al., 2013). There are two circumstances when models extrapolate the occurrence predictions in a location, 1) when the values from one variable are outside of the range of the calibration data (univariate extrapolation), or, 2) when the values are within the range of one variable but represent a new combination when other variables are considered (multivariate combinational extrapolation) (Zurell et al., 2012; Mesgaran et al., 2014) (Figure 4.1). The most accepted practice is thus to report predictions only in locations that show environmental conditions that are within the range of the calibration data (interpolation). However, it is still unclear whether extrapolated predictions are more uncertain than interpolated predictions. By uncertain, I refer to the variability in predictions among several models. More importantly, in some cases extrapolation is needed, particularly when a species niche is poorly known, and/or when assessing the species distributions under novel conditions such as can be found in invaded areas or conditions generated by climate change. To use a SDM in these situations, Elith & Graham (2009) have suggested to determine model reliability by exploring model behaviour when extrapolating and deciding whether it provides a plausible ecological response.

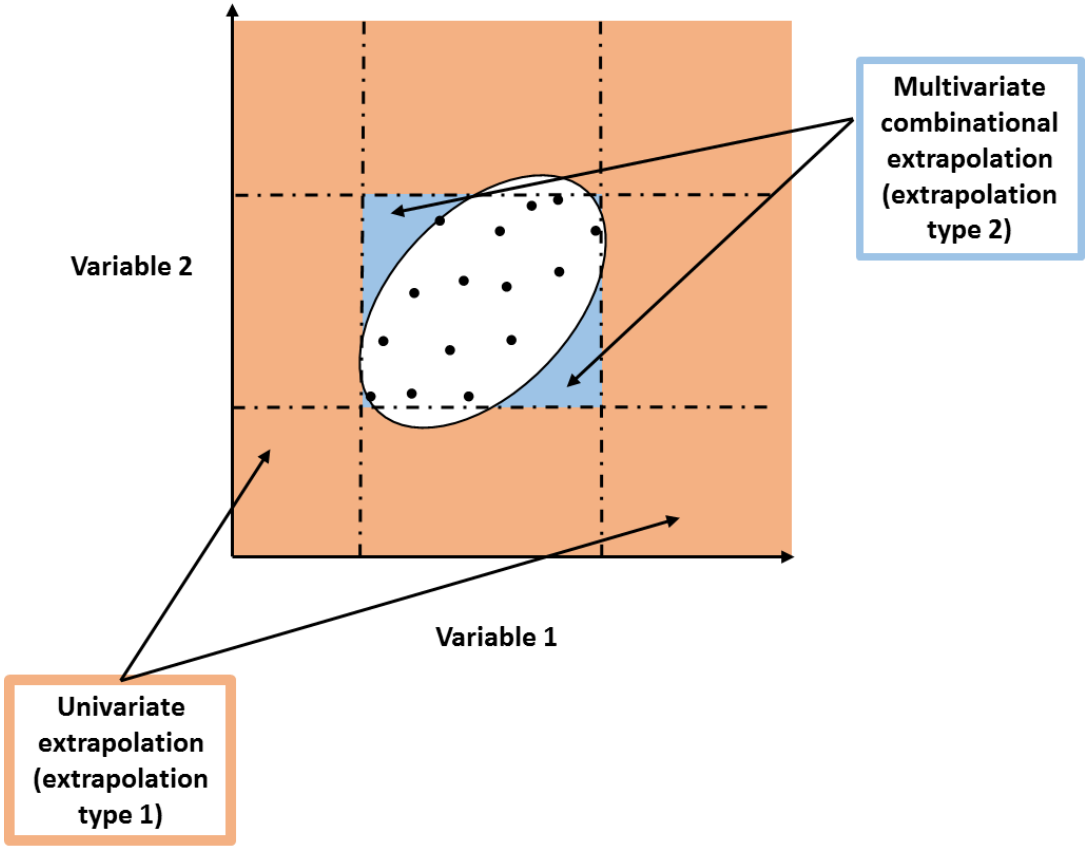


Figure 4.1 Schematic representation of the types of extrapolation in a simplified example of two variables following Mesgaran et al. (2014). Black circles represent occurrence points and the black ellipse defines the "boundary" of the calibration data. The environmental locations that are outside the univariate range (red areas) are considered to be univariate extrapolation (extrapolation type 1). The environmental locations that are within the univariate range but represent a new combination between variables (blue areas) are considered to be multivariate combinational extrapolation (extrapolation type 2).

Numerous studies have investigated the uncertainty in predictions among different models when extrapolating. For example, one of the earliest research articles in the SDM literature that examined the impact of extrapolation on model predictions was done by Thuiller (2003), who detected spatial discrepancies between model predictions when projecting potential future tree distributions in Europe under climate change. Although it is expected that under climate change novel environmental conditions will appear, Thuiller (2003) did not specifically differentiate between interpolated and extrapolated predictions. In another study of uncertainty associated with species distribution prediction under a changing climate, Pearson et al. (2006) found for specific sites where extrapolation occurred, the nine models used predicted the percentage of presence differently for each of four plant species from the Proteaceae family in the West Cape of South Africa. Although

Pearson et al. (2006) found discrepancies when extrapolating, those predictions were not compared to what happens when predictions are obtained by interpolation. While, Godsoe (2010) provided a comparison between interpolated and extrapolated predictions by several SDM, Godsoe (2010) only considered univariate extrapolation. Thus, a need to quantitatively assess and compare uncertainty of species distribution predictions under model interpolation and the two types of extrapolation over a global extent, is indicated.

Additionally, uncertainty under extrapolation has been studied by characterising the relationship between species occurrence and environmental variables (i.e. species response curves). For example, Elith & Graham (2009) and Owens et al. (2013) compared the species response curves of several SDM using virtual species to understand the difference in predictions among models. Their results indicate that models differ based on how they relate species occurrences to environmental variables, particularly when they were used to extrapolate. Indeed, models have three types of behaviour when extrapolating, 1) "clamping" where the last value at the limits of the response surface derived from the calibration data will dictate the extrapolated probability, 2) truncation where response curves are truncated at the limits of the response surface from the calibration data, and, 3) extrapolation in various ways based on the model used (Owens et al., 2013). Although using virtual species helps to gain insight about model behaviour, this approach makes simplifying assumptions on a species niche. Indeed, virtual species niches are usually represented by few environmental variables where species responses are simplified by linear smoothed relationships. Despite these studies a more comprehensive investigation comparing multiple models using a large number of real species is required to give a deeper knowledge about the behaviour of SDMs when extrapolating as well as interpolating. Using real species will test each model's ability to capture the complexity of a species niche. Moreover, there is a clear need to investigate the behaviour of some SDM, under extrapolation, that haven't been explored before and to add further ecological insight to the interpretation of their response curves. Therefore, the objectives of this study were to, 1) evaluate the extent of uncertainty among predictions of species' occurrences when interpolating and extrapolating using 21 invasive freshwater invertebrates as model species over a global extent, 2) determine whether species response curves are ecologically plausible when extrapolating, and, 3) assess the frequency of model interpolation and extrapolation when predicting species' occurrences of the selected species around the world and in New Zealand.

To accomplish these objectives, uncertainty was characterized by the variability in predictions among the models used in this study, herein called predictive uncertainty. Predictive uncertainty should increase when models extrapolate because of the different behaviour, discussed previously, that they could show when extrapolating (Owens et al., 2013). Interpolation and the two types of extrapolation were specifically characterized using a new tool developed by Mesgaran et al. (2014).

To determine if species response curves are ecologically plausible, they were characterized graphically using methods developed by Elith et al. (2005) and Zurell et al. (2012). An attempt was made to identify valid models that despite extrapolation provided ecologically plausible response curves.

4.2 Methods

4.2.1 Predictions of species distribution

Predictions of species distribution for 21 invasive freshwater invertebrates considered in Chapter 2 were used for this study (Table 2.1). In that chapter, nine models from the multimodel framework (Worner et al., 2014) were fitted to a selection of climatic characteristics associated with the presence and pseudo-absence locations, for each species. The predictive models used in this study can be categorized into two types, either data or algorithmic models. A data model formalizes the relationship between occurrences and environmental variables in the form of mathematical equations whereas an algorithmic model (or machine learning model) learns from the data without formalising the relationship between variables (Breiman, 2001b). The models used in the multimodel framework combine four data models: logistic regression (LOG) (McCullagh & Nelder, 1989), naïve Bayes (NB) (McCallum & Nigam, 1998), linear discriminant analysis (LDA) (McLachlan, 1992), and quadratic discriminant analysis (QDA) (McLachlan, 1992), and five algorithmic models : classification and regression trees (CART) (Breiman et al., 1984), conditional trees (CTREE) (Hothorn et al., 2006a), k-nearest neighbours (KNN) (Altman, 1992), support vector machines (SVM) (Cortes & Vapnik, 1995) and artificial neural networks (NNET) (Venables & Ripley, 2002). Models were evaluated using AUC (Area under the curve of the receiver operating characteristic) which is a threshold independent performance metric (Fielding & Bell, 1997). For further details on how the pseudo-absences and variables were selected for each species refer to section 2.2.5.1 and 2.2.5.2 of Chapter 2 respectively. Worldwide predictions were made at a spatial resolution of 10 arc min (0.17°).

4.2.2 Characterizing predictive uncertainty

To characterize predictive uncertainty in species distribution, the standard deviation of the predicted probability among the nine models was computed for each species at each site (Diniz-Filho et al., 2009; Buisson et al., 2010; Briscoe et al., 2016). The use of the standard deviation of prediction to compare different sites can be limited in its application because of the statistic's inherent dependence on mean values (Lewontin, 1966). For example, for unbounded data, large mean values are likely to result in large standard deviations. In such cases, the coefficient of variation (CV) is used. The CV is a relative measure which is computed as the ratio of the standard deviation to the mean (Lewontin, 1966). The advantage of the CV is that it removes the effects of expected changes in the standard deviation due to changes in the mean (Nakagawa et al., 2015). However, the CV does not

work well for bounded data, such as in this study where occurrence probability values go from 0 to 1. The reason is that is that the standard deviation does not increase monotonically with the mean, instead the relationship follows an arc shaped curve reaching maximum variability at intermediate mean values (Figure 4.2). The consequence is that the CV will depict sites with low probability values as being more variable which can mislead the interpretation of the true predictive uncertainty (Figure 4.2). Golay et al. (2013) addressed this issue and proposed an adjusted coefficient of variation for lower and upper bounded data called zeta ζ and it is computed for each site as follows:

$$\zeta_i = \frac{sd_i}{\sqrt{\frac{n}{n-1}}\sqrt{mean_i \times D_i - mean_i{}^2}}$$

where sd_i and $mean_i$ are the standard deviation and mean probability, respectively, for site i, n is the number of models used, and D_i is the difference between the maximum and minimum probability at site i. Zeta is dimensionless and should vary from 0 to 1, where values close to 1 indicate high predictive uncertainty. Zeta was successfully applied in the current analysis because it did not show a relationship with average probability values and therefore was used as a measure of predictive uncertainty (Figure 4.2).

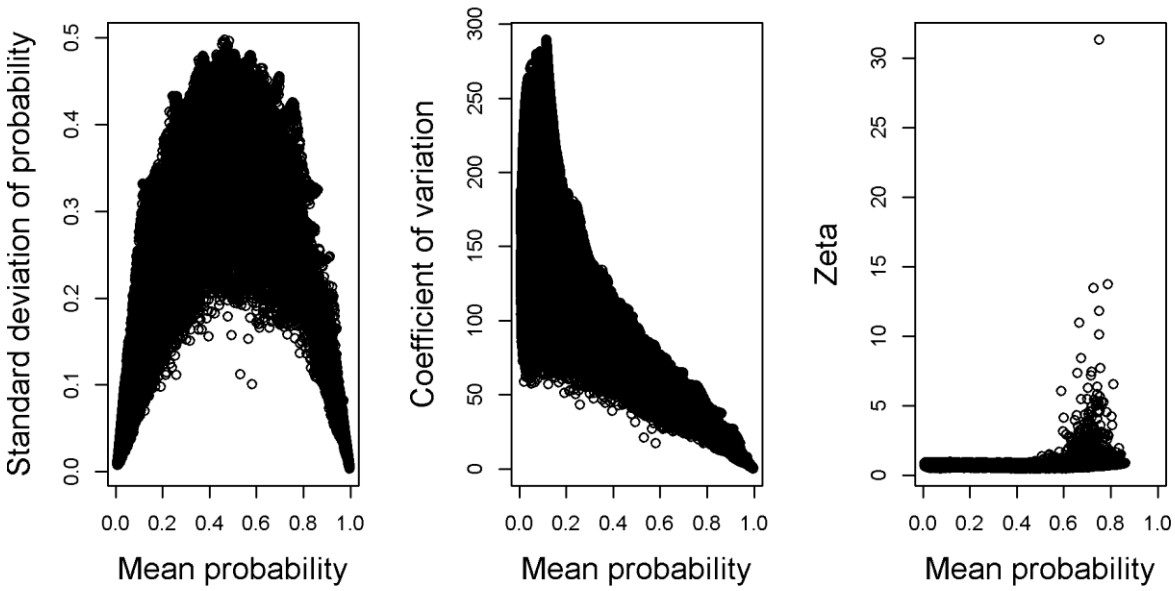


Figure 4.2 Example of the relationship between the standard deviation, coefficient of variation and zeta to mean probability of occurrence. These relationships were obtained from the occurrence predictions of the global distribution for one species (*Corbicula fluminea*). Note that for all the species these relationship were similar.

4.2.3 Describing univariate and multivariate extrapolation in the projection area

To distinguish sites that correspond to interpolation and extrapolation, an extrapolation detection tool (Exdet) developed by Mesgaran et al. (2014) was implemented using their Matlab application ExDet Tool Version 1.0. This method is an alternative to the widely used method MESS (Multivariate Environmental Similarity Surface) (Elith et al., 2010) and modifications by Zurell et al. (2012) and Owens et al. (2013). The advantage of Exdet is that it provides two categories of extrapolation and it also provides the magnitude of extrapolation (Mesgaran et al., 2014). The two types of extrapolation the Exdet tool identifies, are, 1) when the projection data set is outside the range of the calibration data (extrapolation type 1 or univariate extrapolation) and, 2) when there is a novel combination between variables (extrapolation type 2 or multivariate combinational extrapolation) (Figure 4.1). For each grid cell, extrapolation type 1 is computed by first calculating a univariate distance UD for each variable. For any grid cell i and variable j, UD is computed as follows:

$$UD_{ij} = \frac{\min\{P_{ij} - \min(r_j), \max(r_j) - P_{ij}, 0\}}{\max(r_j) - \min(r_j)}$$

where P_{ij} is the variable value for grid cell i and variable j from the projection data and $\max(r_j)$ and $\min(r_j)$ are the maximum and minimum values of that variable for the calibration data. If the values for the variables from the grid cell are within the range of the reference values then UD is zero whereas if values are lower than the minimum or larger than the maximum, UD results in negative values.

The multiple univariate distances UD obtained for each variable are summed and negative values are obtained if the location from the projection data is outside of the univariate range of the calibration data. If a location displays zero extrapolation type 1, they are tested for extrapolation type 2. The calibration data is delimited by drawing an ellipse (or ellipsoid when the number of dimensions > 2). For any grid cell i, extrapolation type 2 is computed as follows:

$$NT2_i = \frac{D_{ei}^2}{D_{r_{max}}^2}$$

where D_{ei}^2 is the Mahalanobis distance of a multivariate point e_i from the centre of the calibration data (centroid of the environmental space) and $D_{r_{max}}^2$ is the maximum Mahalanobis distance of the calibration data that extends from the centroid of the calibration data. The maximum Mahalanobis distance $D_{r_{max}}^2$ is used to draw the ellipse. Values from 0 to 1 indicate similarity in univariate range as well as multivariate combination, where values close to zero are more similar to the calibration data. Accordingly these sites will reveal model interpolation. Values of $NT2$ greater than 1 indicate multivariate combinational extrapolation.

4.2.4 Inflated response curves

Model behaviour was studied by characterizing species occurrence response to the environmental variables to detect when models are generating unreasonable response curves when extrapolating. Visualizing the n-dimensional response space is impossible, thus exploring the response curves for each individual variable used in the model, also known as evaluation strip, has been proposed by Elith et al. (2005). In a recent work, Zurell et al. (2012) suggested an improvement of the evaluation strip, the inflated response plots which help to visualize the response curve of a single variable while also accounting for the minimum, maximum, mean, median and quartile effects of all other variables used in the model. Note that the response curve for one variable therefore comprises several response curves representing all possible combinations of the other variables in the model. Because the number of combinations grows exponentially with the number of variables, a selection of 150 from all possible combinations was performed using a Latin hypercube sampling following Zurell et al. (2012). I focused on the inflated response curves generated for environmental conditions present in New Zealand, thus the characteristics from the calibration dataset and New Zealand were combined to build the inflated response curves. The inflated response curves were generated for each species for a selection of variables that were used to fit the SDM. The selected variables were those that contributed the most to extrapolation across all the locations in New Zealand, because these variables are expected to show a clear contrasting behaviour between interpolated and extrapolated predictions.

The contribution of the variables to extrapolation was computed for each species at each location in New Zealand using methods developed by Mesgaran et al. (2014). For extrapolation type 1 (univariate extrapolation), the variable that contributes the most to extrapolation is the one with the lowest UD (i.e. highest negative value). For extrapolation type 2, the variable that contributes the most to extrapolation is the one with the highest IC_p which measures the percentage of reduction in the Mahalanobis distance when the variable p is dropped. IC_p is computed for each variable as follows:

$$IC_p = 100 \times \frac{D^2_{all} - D^2_{all-p}}{D^2_{all}}$$

where D^2_{all} is the Mahalanobis distance for a point in the presence of all variables and D^2_{all-p} is calculated when variable p is removed. The inflated response curves were generated using code provided by Zurell et al. (2012) and was modified for the models used in this study.

4.2.5 Statistical analysis

To measure the difference of predictive uncertainty between extrapolation and interpolation, a linear mixed effect model (LMM) was used with the package lme4 from R (R Core Team, 2015).

Because a very large sample size can result in a statistically significant effect (small *P*-values), there is an increasing interest in using effect sizes and confidence intervals to avoid the dichotomy of accepting or rejecting the null hypothesis (Nakagawa & Cuthill, 2007; Cumming, 2014). The difference in predictive uncertainty between extrapolation and interpolation was evaluated using effect sizes and their 95% confidence intervals by applying an LMM to subsamples of the dataset. Random sampling without replacement was performed over a global extent, for each species over a total of 120 sites and the samples were combined into one dataset. The sampling was stratified to obtain 40 samples for interpolation, extrapolation type 1 and type 2 locations and was repeated 1000 times. The average and 95% confidence interval (CI) of the regression coefficients were computed across the 1000 regressions. Data from *Aedes albopictus* were removed from the analysis because there were fewer than 40 sites in the extrapolation type 2 category.

Predictive uncertainty measured by ζ was used as a response variable and a variable describing the type of prediction (interpolation, type 1 and type2 extrapolation) was used as a fixed effect. In some locations, extremely high ζ values (greater than 1) were obtained. Closer inspection indicated that these extreme values resulted from mean probability values close to the lower or upper bound (0 or 1). Golay et al. (2013) showed that the reliability of ζ decreased when mean probability is found in those extremes (0-1). To mitigate the potential effect of such extreme ζ values, two sets of linear mixed models were carried out, one with the full range of ζ values and one where the extreme ζ values (>1) were removed.

Genus and family taxonomic groups were used as random effects to account for the non-independence of samples due to taxonomic association (Blackburn & Duncan, 2001). Because it was expected that responses of the same species are not independent, the random effects of the higher taxonomic groupings were tested successively against a separate model using the species name as the single random effect. The final model was selected based on the Akaike Information Criteria (AIC) (Akaike, 1973). Because spatially close sites also violate the independence assumption of linear models, longitude and latitude were added as fixed effects to deal with spatial autocorrelation (Legendre & Legendre, 2012). Visual inspection of the model residuals did not reveal any noticeable deviations from homoscedasticity or normality.

4.3 Results

4.3.1 Predictive uncertainty in interpolated and extrapolated predictions

A comparison of the predictive uncertainty among interpolation and extrapolation categories was made using a linear mixed model. The addition of genus and family groupings to account for non-

independence of samples increased the Akaike Information Criteria (AIC) (Table 4.1), thus the final model used to compare predictive uncertainty had only species as a random effect.

Table 4.1 Mean and 95% Confidence Interval of Akaike Information Criteria (AIC) over 1000 models constructed with different random effects to account for the non-independence of samples due to taxonomic association.

Random effect	Mean	95% CI
Family	-1601.9	[-1738.4,-1465.3]
Genus+Family	-1617.3	[-1754.5,-1480.1]
Genus	-1619.3	[-1756.5,-1482.1]
Species	-1644.4	[-1781.5,-1507.3]

A confidence interval of the estimate that does not overlap with zero is the equivalent to a significant *P*-value in the frequentist sense which is described here as strong support for predictions (Cumming & Finch, 2005). In this study, confidence intervals of the regression coefficients did not overlap with zero implying that there is support for a difference of predictive uncertainty ζ between interpolation and extrapolation locations (Table 4.2). When considering all ζ values, interpolation locations indicated high predictive uncertainty with mean ζ and CI of 0.81 [0.80, 0.82]. Predictive uncertainty ζ increased from the mean interpolation value (intercept) by 0.02 for both extrapolation categories. When the extreme ζ values (> 1) were removed from the analysis, there was still support for an increase of predictive uncertainty ζ from mean interpolation value of 0.04 for both extrapolation categories (Table 4.2).

Table 4.2 Mean predictive uncertainty ζ and 95% CIs around the mean estimated for the interpolation and extrapolation categories using 1000 linear mixed effect models. The response variable was the predictive uncertainty and fixed effects were the type of prediction, longitude and latitude. Two sets analyses were carried out, 1) using the full range of ζ, and, 2) ζ without extreme values (>1).

	ζ			ζ (0-1)		
Fixed effects	β	95% CI		β	95% CI	
Intercept[3]	0.81	0.80	0.82	0.77	0.77	0.77
Extrapolation type 1[4]	0.02	0.02	0.02	0.04	0.04	0.04
Extrapolation type 2[5]	0.02	0.02	0.03	0.04	0.04	0.04

Across global predictions for the 21 species, extrapolation type I (univariate extrapolation) was the most frequent prediction followed by interpolation and extrapolation type 2 (multivariate

[3] Predictive uncertainty for the reference category, interpolation
[4] Difference of predictive uncertainty between reference (interpolation) and extrapolation type1.
[5] Difference of predictive uncertainty between reference (interpolation) and extrapolation type2.

combinational extrapolation) (Figure 4.3). For New Zealand, interpolation was predominant, followed by extrapolation type 1 predictions which showed high variability among species, finally followed by extrapolation type 2. Multivariate combinational extrapolation was rare worldwide including New Zealand.

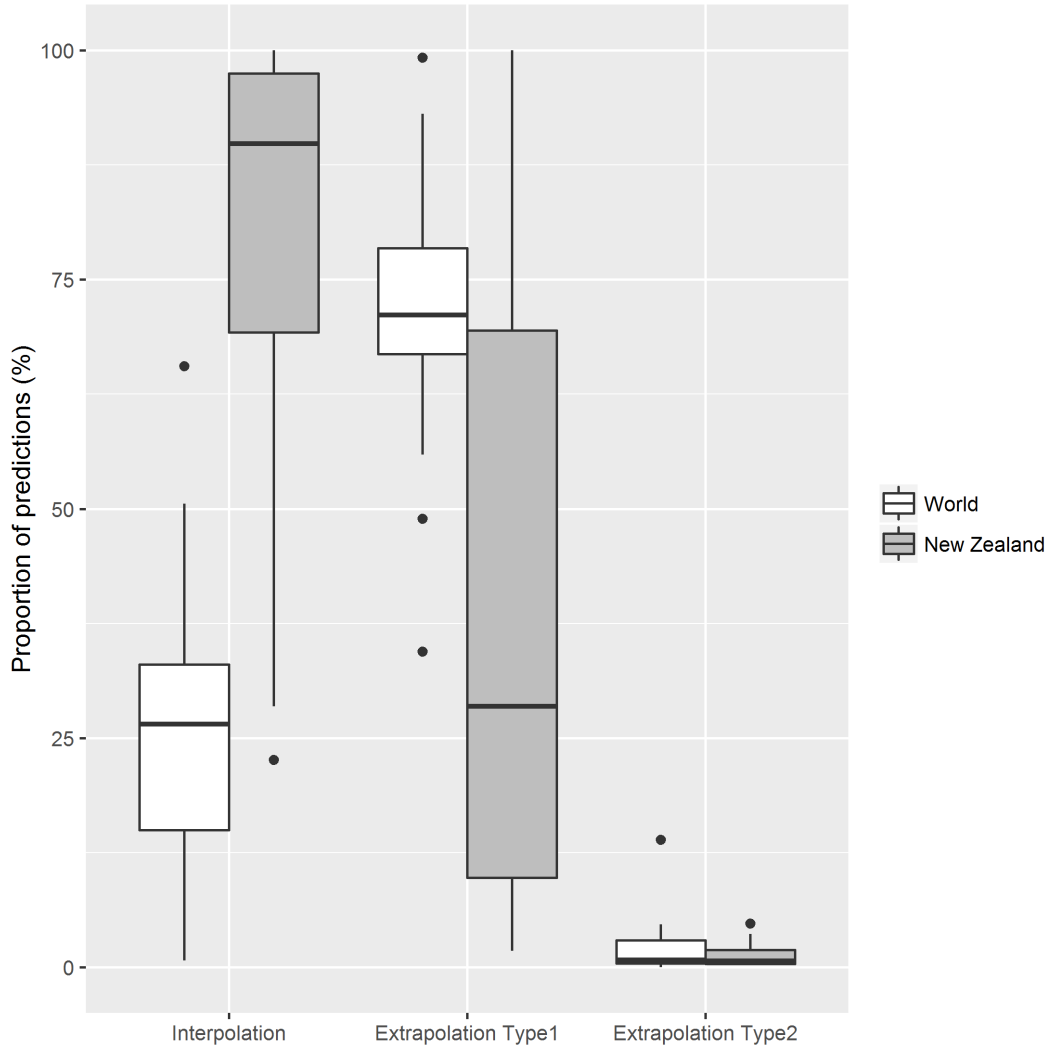


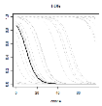
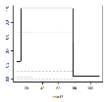
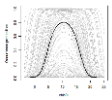
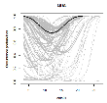
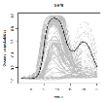
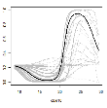
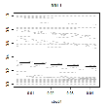
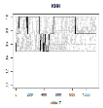
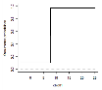
Figure 4.3 Proportion of occurrence predictions corresponding to each category of prediction: interpolation, univariate extrapolation (extrapolation type 1) and multivariate combinational extrapolation (extrapolation type 2). Occurrence predictions were obtained for the world and for New Zealand for 21 invasive freshwater invertebrates.

4.3.2 Inflated response curves for variables contributing the most to extrapolation

Model behaviour was studied using inflated response curves which revealed that each model fits different curves. The main types of curve observed are presented in Table 4.3. The response curves for each individual species and selected variables are presented in Appendix B.1. Logistic regression showed a narrow range of curves which is expected when no polynomial terms (second and third order) are added. Some models provided overly complex response curves which do not seem

ecologically realistic but are the result of peculiarities of the sample data. NNET, for example, showed complex patterns, probably indicating overfitting as a result of fitting noise or data deficiency (Table 4.3, Appendix B.1). Despite this, NNET showed flexibility by fitting a wide range of curve shapes (Table 4.3). KNN provided complex response curves as well, but unlike NNET, the response does not seem to describe an actual ecological response or the result of fitting noise (Appendix B.1). KNN is a clustering technique where the probability of a location belonging to a class is voted by the closest k neighbour classes so there is no assumption about the shape of the response curve. SVM showed similar flexibility to NNET, particularly representing unimodal and bimodal response curves. CART and CTREE tended to show abrupt curves with a sudden increase or decrease of occurrence probability, or squared unimodal curves (Table 4.3). This behaviour is explained by how these models classify data. Observations are split into nodes at established threshold values of each variable to form a decision tree. Flat trends along an environmental variable indicate that, according to the model, this variable does not contribute to the occurrence of the species. Interestingly, these flat trends were observed in all models but not for the same variables.

Table 4.3 Inflated response curves fitted by the models used in the multi framework (Worner et al., 2014). The figures are illustrations of the type of inflated response curves observed when estimating the probability of occurrence across a selection of variables. The inflated response curves for each species and variable can be found in Appendix B.1.

		Model								
Type of curve		LOG	NNET	CART	QDA	LDA	NB	CTREE	KNN	SVM
Logistic		x	x		x	x	x			x
Squared unimodal				x				x		
Unimodal			x		x		x			x
Unimodal decrease					x					
Bimodal			x							x
Bimodal increase/decrease										x
Linear		x				x				
Flat trend		x	x	x	x	x	x	x	x	x
Complex			x					x	x	x
Abrupt increase/decrease		x	x	x				x	x	

One of the main objectives of plotting the inflated response curves was to select models that predict reasonable response curves when extrapolating as suggested in Zurell et al. (2012). In their example, Zurell et al. (2012) compared only two types of models, generalized additive models and boosted regression trees, where both types of model behaved similarly when interpolating and differed slightly when extrapolating. In this study, in some cases, the nine models showed different response curves for the same environmental variable (Appendix B.1) making it a challenge to detect which models provide reasonable response curves when extrapolating.

4.4 Discussion

This study addresses a critical problem in the predictions of species distribution regarding the uncertainty of extrapolation. This work characterized quantitatively and qualitatively the uncertainty in predictions of species distributions. For the first time, a quantitative comparison was performed between interpolation, univariate and multivariate combinational extrapolation predictions at a global extent using several species. Moreover, model behaviour was characterized to identify models that provide ecologically plausible responses to environmental variables.

4.4.1 Uncertainty in extrapolated and interpolated predictions

Surprisingly, model interpolation showed large predictive uncertainty (Table 4.2), that resulted in a small increase when compared to model extrapolation. Interestingly, both types of extrapolation, univariate and multivariate combinational extrapolation, showed the same increase of predictive uncertainty in relation to interpolation. The high degree of uncertainty when interpolating and extrapolating was also revealed when inflated response curves were examined (Appendix B.1). In some cases, each model produced a different response curve for the same variable revealing the variety of modelling approaches represented by the nine models within the multimodel framework (Worner et al., 2014).

Considering that all the models used in this study had similar predictive performance measured by AUC in the training data (Appendix B.2), it was surprising to find such high interpolation predictive uncertainty. Similar results were found by Thuiller (2003), where similar performing models gave different spatial predictions. It seems, therefore, that small differences in performance metrics may result in large differences in spatial predictions. While these performance metrics did not reveal extreme differences between methods, such differences became clear when observing the inflated response curves. Therefore, these results highlight the importance of combining several approaches to evaluate models and reinforce the need to develop a spatial measure of performance.

Few studies have specifically investigated predictive uncertainty between interpolation and extrapolation. Most studies largely comprise visual assessments of model agreement such that conclusions needed a more rigorous assessment to be validated. For example, in a study of range shifts in 61 European trees under climate change, Thuiller (2003) using a visual assessment, found spatial discrepancies among four models when predicting current distribution but these differences were even more accentuated when predicting future distributions. However Thuiller (2003) did not specifically describe interpolation and extrapolation. On the other hand, Zurell et al. (2012) made a distinction between interpolation and extrapolation areas and found that both generalized linear models and boosted regression trees predicted similarly within the sampled environments but

differed under novel environmental conditions when investigating inflated response curves and visual assessment of spatial predictions. These examples and the empirical evidence provided in this study highlight that predictive uncertainty seems to be more prominent when extrapolating but depending on the models used, large discrepancies can be observed in interpolation areas as well. Differences in interpolation can be explained by the different underlying functions fitted by the methods, the quality of the distribution data and how important the environmental variable actually is for explaining the presence of the species (Elith & Graham, 2009). Using a virtual species, Elith & Graham (2009) found that most of the models they studied, correctly represented the species' response for strong environmental trends which are dominant drivers of the species' distribution. They also determined that some models were not able to characterize the true response curve properly when sampling along an environmental gradient that was too sparse.

Discrepancies in extrapolation will depend on how the model is constrained to extrapolate. Some models are known to "clamp" or truncate predictions , or show different types of response curves when extrapolating (Owens et al., 2013). The inflated response curves were used to understand model behaviour and detect when models are predicting erratically when extrapolating. However, the variety of response curves made it impossible to select which models provide sensible response curves for extrapolation. Several studies have assessed the behaviour of LOG as well as other models using virtual species (Elith & Graham, 2009; Zurell et al., 2012; Owens et al., 2013). For the specific case of LOG and the virtual species generated by Elith & Graham (2009), their study indicated nonsensical ecological responses when extrapolating because the model was fitted using polynomials and cubic functions. Further investigation using a virtual species approach is required to understand model behaviour when extrapolation occurs for the methods used in the multi-model framework.

There are two emerging viewpoints in the SDM literature where some authors recommend to use simpler models with clear ecological interpretation whereas others focus more on predictive accuracy using complex methods (Austin, 2007; Merow et al., 2014). In this current study, some of the methods used showed they were compatible with ecological theory. Both data and algorithmic models represented theoretical species responses, such as smoothed unimodal and bimodal bell-shaped responses (Table 4.3). Gauch & Whittaker (1972) proposed that unimodal bell-shaped curves represent physiological limits along environmental gradients whereby occurrence suitability drops when moving away from the optimum. On the other hand, Müller-Dombois & Ellenberg, (1974) hypothesised that bimodal response curves can be the result of species physiological optima been displaced by a superior competitor. However evidence for the bell and bimodal shape curves is scarce (Austin, 2002). For example, Austin (1987) found that eucalypt species indicate positive skewed curves along a temperature gradient in southern New Wales.

Response curves can also have different behaviour at both extremes of the environmental factor, where at one extreme an abrupt decrease of the function can be observed whereas at the other extreme a gradual decrease can occur (Merow et al., 2014). In the current study, CTREE and CART both showed a simplistic ecological response such as squared unimodal or an abrupt increase or decrease. Linear response curves such as the ones observed for LOG and LDA can be detected when the environmental range has been partially sampled, representing for example, only one side of a unimodal response (Merow et al., 2014). Flat trends generated by some models (Table 4.3) may reveal that the variable has a weak influence on the suitability of the species or that the signal is too weak to be detected by those models. These trends could also indicate that models are weighting the variables differently (Capinha et al., 2011).

On the other hand, the other machine learning methods such as KNN, NNET and SVM, generated overly complex curves containing several inflections and turning points compared the smoothed response curves generated by data models such as LOG, NB, LDA and QDA (Table 4.3). Complex species-environment relationships are not necessarily incompatible with ecological theory but rather may represent patterns such as variability of individual responses or different life stages that have been pooled together in the occurrence data (García-Callejas & Araújo, 2016). Other researchers have hypothesised that complex response curves may result from a representation of the realized niche and that a smooth species response is more related to the representation of the fundamental niche (Huntley et al., 1995; Soberón, 2007). Complexity may be problematic if flexible models such as machine learning techniques are overfitting data, in other words are capturing peculiarities of the data and not the true underlying process (Elith & Graham, 2009; Bell & Schlaepfer, 2016). However, insufficient flexibility will result in a misrepresentation of the species-environment relationship (Merow et al., 2014). Thus, it is crucial to identify models that are capable of distinguishing ecological processes in sample data from environmental noise. Therefore appropriate model evaluation is needed in order to select those that are capable of generalizing and not overfitting. Accordingly, other evaluation methods that achieve this objective will be tested in future work (Chapter 5).

4.4.2 Practical implications

When using an ensemble approach which is when several models are used to determine the probability of occurrence of a species, numerous ways of combining predictions exist (Marmion et al., 2009). This study challenges the use of an ensemble approach when predictions from several models are averaged because of the high predictive uncertainty found both in interpolation and extrapolation. Decisions made with respect to invasive species surveillance and management are likely to have high predictive uncertainty if they are based on averaged predictions when models

with such different assumptions are combined. Thus when using such a diverse set of models, predictions can be combined using other types of ensemble methods. For example, the PCA approach enables models that are predicting similarly to be identified and thus predictions can be combined by averaging or using the median (Marmion et al., 2009). By combining models with similar assumptions, such as models generating complex versus simple species response curves, one can provide different prediction scenarios.

With regard to extrapolation, as discussed in previous studies, the most conservative approach is to detect extrapolation areas using tools such as Exdet (Mesgaran et al., 2014) and avoid interpretation in those areas (Fitzpatrick & Hargrove, 2009; Owens et al., 2013). Others have suggested that the degree of extrapolation can be reduced by calibrating models at the largest extent available. For instance, Pearson et al. (2002) trained NNET at a European scale to include a wide climatic range and then downscaled predictions at finer resolution in Great Britain. Nevertheless, this may not work in all circumstances, particularly for future projections where global conditions could be entirely novel (Fitzpatrick & Hargrove, 2009). Finally, some authors consider that a solution to extrapolation is to use mechanistic models where the full response curves are captured and can be used beyond the observed data but such models are more time consuming to determine as well as implement (Kearney et al., 2009; Merow et al., 2014). Extrapolation may be necessary in some cases and could be used, provided some ecological insight and knowledge of model behaviour are used to assist interpretation. The most interesting application of species distribution models is the transference of the species response to novel conditions where no information is available. In fact, for some species where sampling is particularly difficult, such as in tropical areas, suitable areas will be often identified by extrapolation (Carneiro et al., 2016). For the current case study of twenty-one freshwater invertebrate species, the global projections were mainly obtained by extrapolation, whereas in New Zealand by interpolation (Figure 4.3). The methods used in this study enable the spatial characterization of how the predictions were obtained (by interpolation or extrapolation). For now, extrapolated predictions need to be interpreted with care until there is a greater understanding of model behaviour when extrapolation occurs.

4.5 Conclusion

This study characterized quantitatively and qualitatively, uncertainty around interpolation and univariate and multivariate combinational extrapolation when using SDM on real species over a large extent. High uncertainty in predictions of species occurrence existed when models interpolate as well as when they extrapolate, although slightly more for the latter. Further understanding about uncertainty was gained by characterizing model behaviour for a selection of nine SDM. Because of the high uncertainty found in interpolation, some concerns regarding classical model evaluation

techniques have been raised. Thus, it is recommended to study a model's predictive ability by investigating predictions and model behaviour as shown in this study. Different predictive methods have their advantages but averaging their predictions may hinder decisions for surveillance and management. I suggest combining predictions using ensemble techniques after grouping models with similar response curves to provide different views of the risk of establishment of invasive species. Even though there is a general view presented against making predictions in extrapolation areas, this research confirmed how frequently models extrapolate, particularly for worldwide predictions. Provided that models predictive ability is thoroughly tested as shown in this research, only then one can determine model behaviour and whether predictions of species distributions are appropriate for the intended applications.

Chapter 5

Towards an improved framework for evaluation of correlative species distribution models

5.1 Introduction

Correlative species distribution models (SDM) have been widely used to understand fundamental ecological questions such as the drivers of species' range changes as well as they are valuable tools to study the impact of climate change, species conservation and invasive species management (Zimmermann et al., 2010). These models represent the realized niche, or the set of environmental conditions in which a species can survive and persist, by relating occurrence information with environmental variables (Hutchinson, 1957; Guisan & Zimmermann, 2000). Despite this wide use, SDM will only be truly useful if they provide some degree of generalizability (Vaughan & Ormerod, 2005; Wenger & Olden, 2012), also known as transferability to new conditions (Randin et al., 2006; Peterson et al., 2007). More specifically, models show transferability when they are able to predict datasets other than the ones used for their development. Thus, species-environment relationships characterized by such models should correctly reflect species' distributions in new areas or different time periods. The challenge however is to identify models that actually show transferability. Current methods to evaluate models suffer from several problems that can result in a misinterpretation of model's ability to transfer predictions to new conditions and therefore decisions based on those models may be misleading.

The fundamental problem of model transferability lies within the well-recognised heterogeneity of ecological processes (Wenger & Olden, 2012). Factors such genetics, phenotypic plasticity and variable biotic interactions can lead to change in species-environment relationships across time and space (Randin et al., 2006; Bahn & McGill, 2013; Godsoe et al., 2015). Given the heterogeneity in ecological processes, it can be vital to choose a model of suitable degree of complexity. Inappropriate specification of model complexity will result in overfitted or underfitted models, which can lead to failure in transferability (Wenger & Olden, 2012; Radosavljevic & Anderson, 2014). An overly complex model can fit the data too well, describing noise or sampling bias which results in overfitting. On the other hand, underfitting occurs when a model is too simple and therefore, unable to capture the true underlying relationship (Merow et al., 2014). Both overfitted and underfitted models will fail to generalize species-environment relationships, thus their predictions of new datasets may be unreliable. Another methodological challenge to achieving transferability is when predictions are made in novel conditions that are different from those to

which the models were calibrated (Bahn & McGill, 2013; Radosavljevic & Anderson, 2014). Predictions in this latter context are extrapolated and there is controversy as to whether the practice of extrapolation is appropriate because of the lack of knowledge of the species' response under the novel conditions (Fitzpatrick & Hargrove, 2009; Owens et al., 2013). The identification of transferable models is therefore critical if predictions are to be used in new areas or time periods. However, model evaluation methods suffer from several issues related to the dependence between the calibration and test dataset, which can prevent the identification of transferable models.

Any SDM's ability to predict is measured by the predictive success of species' distribution (*i.e.* model performance). Typically, the data are randomly divided so that one subset is used for model calibration and the other subset is used for model testing. This process is repeated several times and model performance predicting test data is averaged across the number repetitions (random cross-validation). However, in most of the cases, random cross-validation is not necessarily an adequate test for model transferability. First, this method does not necessarily ensure that the test data will be independent from the calibration data because occurrences in both datasets are usually spatially autocorrelated (Veloz, 2009; Hijmans & Hall, 2012; Bahn & McGill, 2013). Spatial autocorrelation refers to the fact that locations that are close together tend to be similar. As a result, occurrences used for model calibration are not necessarily independent from those used in the test data. This will lead to an overestimation of the performance measure because models are already optimized to predict the test dataset (Veloz, 2009; Bahn & McGill, 2013). Second, a dependence between the calibration and test data may emerge when generating pseudo-absences. For correlative SDM that require absences, pseudo-absences are often generated in a geographic background, that is the study area where SDM are calibrated (Chapter 2). Several pseudo-absence techniques are available; one which is widely used involves performing an environmental profiling on the data (Engler et al., 2004; Senay et al., 2013). In this case, pseudo-absences are selected through a comparison between the environmental characteristics of the geographic background and presences. However, if pseudo-absences are generated using the whole geographic background, some pseudo-absences selected for model testing may include information from the geographic background used in the calibration data. This could also result in an inflation of the performance measure.

Ideally, models should be tested using independent data collected from another data collection instance or from another time (although under certain circumstances this may not guarantee independence) but this information is rarely available (Araújo & Guisan, 2006; Elith et al., 2006). There are, however, other ways to generate more independent calibration and test datasets in order to rigorously evaluate model performance. Generating spatially structured datasets involves non-randomly dividing the data into subsets for cross-validation in such a way that spatial dependence between calibration and test datasets is reduced, this is, hereafter called non-random

cross-validation (Wenger & Olden, 2012; Bahn & McGill, 2013). For pseudo-absences, some authors have attempted to increase independence by masking some portions of the geographic background where the pseudo-absences are generated to avoid introducing information from the calibration data in the test dataset (Radosavljevic & Anderson, 2014).

The use of non-random cross-validation in the SDM literature is not standard practice yet but it has clearly attracted more interest (Wenger & Olden, 2012; Bahn & McGill, 2013; Radosavljevic & Anderson, 2014). More recently, an R package was developed to generate spatially structured datasets (ENVeval, Muscarella et al., 2014). When using non-random cross-validation, thereby decreasing the dependence, several studies found that the performance of SDM decreases in comparison to conventional cross-validation (Wenger & Olden, 2012; Bahn & McGill, 2013; Radosavljevic & Anderson, 2014). Major gaps remain in our understanding of the dependence of calibration and test datasets which need to be addressed in order to validate non-random cross validation. While the decrease in model performance found when using non-random cross-validation was associated with the greater independence between the calibration and test datasets, no examination was performed to check whether it was related to predicting on novel conditions (extrapolation). Additionally, it is still unclear which procedure is best to generate spatially structured datasets in non-random cross-validation. So far, very little attention has been paid on the potential dependence that pseudo-absence generation strategies could create between calibration and test datasets. Thus an assessment of the effect pseudo-absence strategy on model performance is critical to identify a rigorous framework of model evaluation.

For all the reasons discussed previously, it is crucial to improve model evaluation by investigating the different problems related to evaluating models and determine the best methodology for a rigorous assessment of model transferability. An improved framework will allow modellers to detect when models are not able to transfer predictions to new areas/times and thus likely to compromise decisions related to species management.

The overall aim of this study was to measure the effect of the dependence between calibration and test data on model performance. I compared model performance when pseudo-absences were generated by masking or by including the whole geographic background, along with different model evaluation methods (random cross validation and non-random cross validation). The work in this chapter evaluated the performance of nine SDM across 14 species. The specific objectives were to, 1) compare the performance of the models for two pseudo-absence generation strategies (whole background versus masked background) and two evaluation methods (random versus non-random cross validation), 2) determine whether extrapolation has occurred using the two evaluation

methods, 3) determine the best procedure for generating spatially structured datasets, and, 4) use this procedure to identify models that have high transferability.

First I measured the effect the dependence between calibration and test datasets generated by the pseudo-absence generation strategy. I hypothesized that when comparing the conventional method (using whole the geographic background) against the proposed method (masking the geographic background), a decrease in model performance will be observed as a result of reducing the dependence between the calibration and tests datasets. Similarly, a decreased model performance when comparing random-cross validation against non-random cross validation would indicate a reduction of the dependence between the calibration and test datasets. A comparison of environments between the calibration and test datasets was performed to confirm that any decrease in model performance was not related to extrapolation (predicting occurrences in novel environments).

5.2 Methods

5.2.1 Species occurrences and environmental variables

Twenty-one invasive freshwater invertebrates, described in Chapter 2 were selected for this study (Table 2.1, Chapter 2). For each species' dataset, only one occurrence point per grid cell of resolution 10 arc minutes (0.17°) was used to reduce spatial autocorrelation to some extent (Veloz, 2009; Kramer-Schadt et al., 2013). The environmental characteristics associated with the occurrence data were extracted from the Climond database (Kriticos et al., 2012). Twenty seven variables were selected which reflect average, extreme and seasonality of hydrothermal conditions (Table 2.2, Chapter2).

5.2.2 Non-structured and spatially-structured datasets

To test the effect on model performance of the dependence between the calibration and test datasets, each species dataset was either used as a whole (non-structured) or was spatially divided into subsets (spatially-structured). For the latter, each presence dataset was divided into equal sized groups based on latitude or longitude (Figure 5.1). Following recommendations by Wenger & Olden (2012) datasets were divided into ten subsets because data coverage was good (at least 50 occurrences). To stratify the datasets into 10 equally sized subsets, every 10th percentile longitude/latitude of all presences was computed and used to split the dataset.

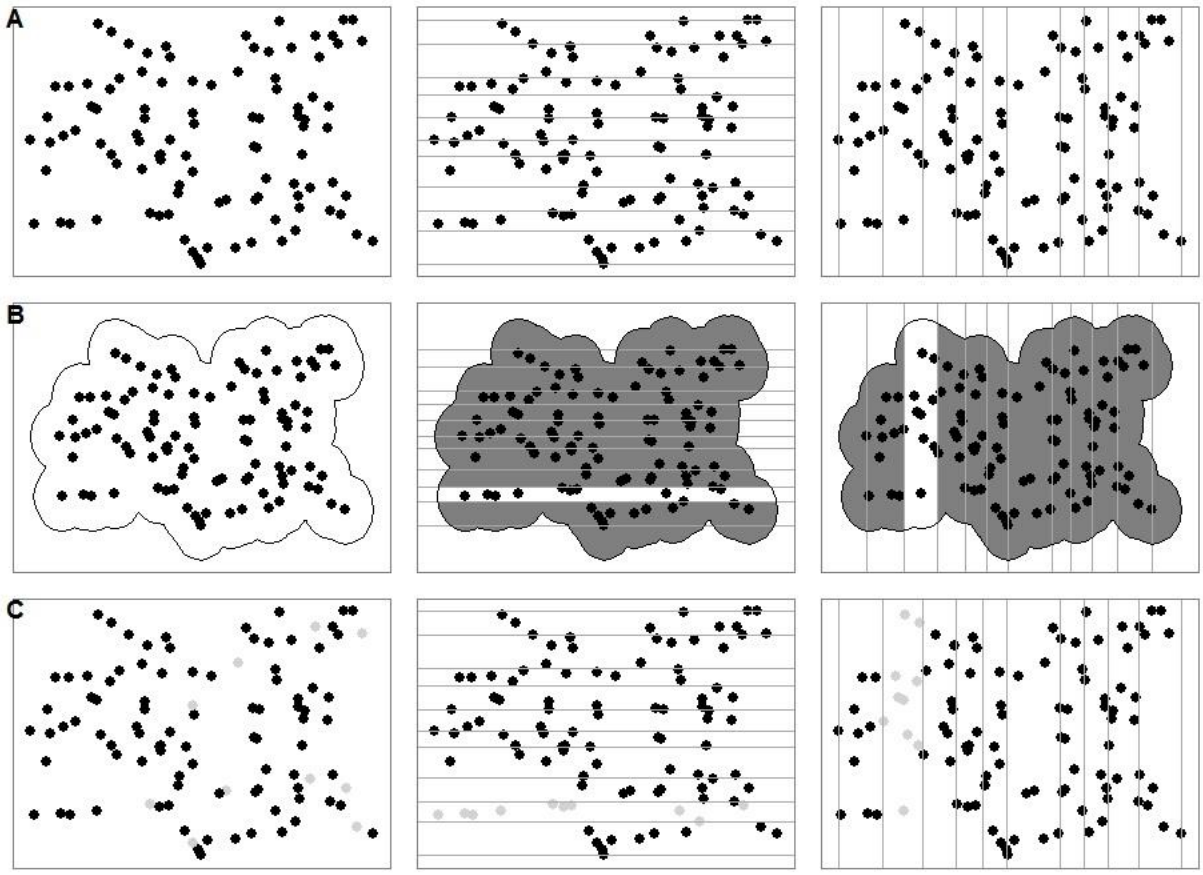


Figure 5.1 Schematic representation of data stratification. Black circles indicate where the species is present, grey lines indicate dataset subsets and the black line delimits the geographic background where pseudo-absences were generated. Panel (A) represents the general stratification of the datasets. On the left, the dataset is non-spatially structured and in the centre and right, the dataset is spatially structured in latitudinal and longitudinal subsets, respectively. Panel (B) represents the pseudo-absence generation methods. On the left, the whole geographic background is used for generating pseudo-absences. In the centre and on the right, parts of the geographic background are masked (grey) using latitudinal and longitudinal subsets respectively. Pseudo-absences are thus generated using only information from the white part of the geographic background. The masking procedure is repeated for each division. Panel (C) represents the model evaluation methods. On the left, data are randomly divided where one part was used for model calibration (black circles) and the other part for model testing (grey circles). In the centre and right, data was non-randomly divided using the latitudinal and longitudinal subsets respectively, where one part was used for model calibration (black circles) and the other for model testing (grey circles).

5.2.3 Masked and non-masked pseudo-absence generation

Pseudo-absences were generated using the three step method from Senay et al., (2013) and Worner et al. (2014) and explained in detail in section 2.2.5.1 (Chapter 2). The pseudo-absences were generated over a geographic background by selecting environments that were outside of the species' realized niches (Worner et al., 2010; Senay et al., 2013). First, this method delimits the extent of the

geographic background by looking at an appropriate distance where the environmental variables show similar correlation structure. Second, locations that were environmentally dissimilar to the presences were identified using the OCSVM algorithm (one class support vector machine) (Schölkopf et al., 2001). Third, a subset of the pseudo-absences are selected using a kmeans algorithm (Lloyd, 1982), where the final number is equal to the number of presences. The OCSVM algorithm did not converge for seven species as a result they were removed from the analysis. The fourteen species used in this study are listed in Table 5.1.

Table 5.1 List of the species studied and their number of occurrences.

Species	Number of occurrences
Aedes albopictus (Skuse, 1895)	2975
Bithynia tentaculata (Linnaeus, 1758)	1046
Bythotrephes longimanus (Leydig, 1860)	516
Corbicula fluminea (O. F. Müller, 1774)	1409
Dreissena polymorpha (Pallas, 1771)	1468
Dreissena rostriformis bugensis (Andrusov, 1897)	240
Eriocheir sinensis (Milne-Edwards, 1854)	1046
Gammarus tigrinus (Sexton, 1939)	293
Orconectes limosus (Rafinesque, 1817)	881
Orconectes virilis (Hagen, 1870)	547
Pacifastacus leniusculus (Dana, 1852)	546
Pomacea canaliculata (Lamarck, 1828)	236
Procambarus clarkii (Girard, 1852)	490
Valvata piscinalis (Muller, 1774)	1001

Masked and non-masked methods select pseudo-absences from the geographic background in different ways. For non-masked generation, the pseudo-absences were generated across the whole geographic background using the whole, non-structured dataset (Figure 5.1). For the masked dataset, pseudo-absences were generated in the background of each previously delimited longitudinal or latitudinal subset (structured dataset) while masking out the other subsets (Figure 5.1). This was done to ensure that pseudo-absences were generated using only information from the geographic background corresponding to respective subset, thereby increasing the independence between calibration and test datasets. Thus, three datasets of presences and pseudo-absences were created for each species (non-masked, longitudinal and latitudinal masked).

5.2.4 Variable selection and modelling techniques

For each of the three datasets generated for each species, a subset of the twenty-seven variables was selected using random forests (Breiman, 2001; Worner et al., 2014, Chapter2) and are shown in

Appendix C.1. Nine models were used to estimate the occurrence probabilities: 1) logistic regression (LOG) (McCullagh & Nelder, J. A, 1989), 2) classification and regression trees (CART) (Breiman et al., 1984), 3) conditional trees (CTREE) (Hothorn et al., 2006a), 4) k-nearest neighbours (KNN) (Altman, 1992), 5) naïve Bayes (NB)(McCallum & Nigam, 1998), 6) support vector machines (SVM)(Cortes & Vapnik, 1995), 7) artificial neural networks (NNET) (Venables & Ripley, 2002) , 8) linear discriminant analysis (LDA)(McLachlan, 1992), and, (9) quadratic discriminant analysis (QDA) (McLachlan, 1992).

For models that require prior parametrization (KNN, SVM and NNET), several parameter sets were tested using 10-fold random cross validation repeated 200 times. The initially tested parameters and final parameters are given in Appendix A.4 and Appendix C.2, respectively. Only random cross-validation was used for model parametrization because assessing the effect of model evaluation on parametrization was out of the scope of this study.

5.2.5 Model evaluation using random and non-random cross-validation

Model performance was assessed using a threshold-independent measure, the root-mean-squared error (RMSE) (Caruana & Niculescu-Mizil, 2004). The RMSE was selected for the final interpretation because, 1) it is not affected by an imbalance of presences and absences, unlike the AUC metric (Lobo, 2008), and, 2) the distribution of RMSE (its normality and homoscedasticity) was judged to be more appropriate than other performance measures for statistical analysis. Despite this, other performance measures were tested and the interpretation of the results did not change (Appendix C.3). RMSE measures the deviation of predictions from observed occurrence (presence or pseudo-absence) and is computed as follows:

$$RMSE = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(p_i - o_i)^2}$$

where o_i and p_i are the observed occurrence and the predicted probability of species occurrence respectively, at site i in the test dataset, n is the total number of sites within the test dataset.

For the three datasets for each species (non-masked, longitudinal and latitudinal masked), model performance was measured using 10-fold random and non-random cross-validation. Random cross-validation was repeated 200 times, which involved randomly dividing the data in 10 folds, where 9 folds were used for model calibration and 1 fold for model testing (Figure 5.1). This was repeated until all folds were tested. For non-random cross-validation, the testing procedure was similar, however, the folds were obtained from the spatially-structured datasets (Figure 5.1) and only

one repetition was performed. Note that latitudinal or longitudinal folds are the same subsets used for the masked background generation technique (Figure 5.1).

5.2.6 Extrapolation detection within random and non-random cross-validation

To verify whether models are extrapolating at each evaluation test, the extrapolation detection tool (Exdet) was used from the ecospat package in R (see section 4.2.3 Chapter 4 for further details, Mesgaran et al., 2014; Broennimann et al., 2015; R Core Team, 2015). The advantage of Exdet is that it provides two categories of extrapolation and it also provides the magnitude of extrapolation (Mesgaran et al., 2014). The two types of extrapolation the Exdet tool identifies, are, 1) when the projection data set is outside the range of the calibration data (extrapolation type 1 or univariate extrapolation) and, 2) when there is a novel combination between variables (extrapolation type 2 or multivariate combinational extrapolation) (Figure 4.1, Chapter 4). This tool measures the distance between the calibration and test datasets using a univariate and multivariate distance (Mahalanobis distance). Exdet values between 0 and 1 indicate that predictions were not extrapolated, where values closer to zero are more similar to the calibration dataset. On the other hand negative values indicate extrapolation type 1 and values greater than 1 indicate extrapolation type 2. Extrapolation detection was performed for random and non-random cross-validation (longitudinal and latitudinal).

5.2.7 Statistical analysis

R statistical software (R Core Team, 2015) and the lme4 package (Bates et al., 2015) were used to perform a linear mixed effects analysis of the relationship between model performance and the different pseudo-absence and evaluation techniques which were treated as fixed effects. Modelling techniques were also included as fixed effect to account for other sources of variation and species was included as a random effect. A linear mixed effects analysis was also performed to test the relationship between distance of calibration-test datasets and the evaluation technique, which was treated as a fixed effect and species was treated as a random effect. Visual inspection of the model residuals did not reveal any noticeable deviations from homoscedasticity or normality.

To account for the non-independence of samples due to taxonomic association, genus and family taxonomic groups were also used as random effects (Blackburn & Duncan, 2001). Because it was expected that responses of species belonging the same genus were not independent, the random effects of the higher taxonomic groupings were tested successively against a reference model using species name as a random effect. The final model was selected based on the Akaike's Information Criterion (AIC) (Akaike, 1973). The 95% confidence intervals around the model parameters were obtained by parametric bootstrapping (n = 1000) as recommended by Bates et al. (2015).

5.3 Results

5.3.1 Model performance among pseudo-absence and model evaluation techniques

The aim of this work was to test the effect of pseudo-absence generation and model evaluation methods on model performance, which were both treated as fixed effects in the linear mixed effect model. To account for other sources of variation, notably modelling technique was treated as fixed effect and species as random effect. The addition of the genus and family groups as random effects to account for non-independence of samples, resulted in higher AIC values, thus, the final model only contained species as a random effect (Table 5.2).

Table 5.2 Akaike's Information Criterion (AIC) for the two sets of linear mixed models, one for analysing the relationship of model performance (model1) and the second for analysing the relationship of distance between calibration-test datasets. All models were constructed with species as random effect and other random effects were successively added to account for the taxonomic non-independence of the samples.

Random effect	AIC model 1	AIC model2
Genus+Family	-2823.1	-138734.3
Genus	-2825.0	-138736.3
Family	-2825.1	-138736.3
Species	-2826.8	-138738.3

The masked pseudo-absence generation method resulted in a significant decrease in model performance (*i.e.* increase in RMSE), as shown by the confidence intervals, in relation to the non-masked pseudo-absence generation (Figure 5.2). This suggests that model performance may be overestimated *(i.e.* RMSE may be underestimated) because of the lack of independence when pseudo-absences are generated across the whole background. Both longitudinal and latitudinal masked methods indicated similar increase of RMSE in comparison to the non-masked method.

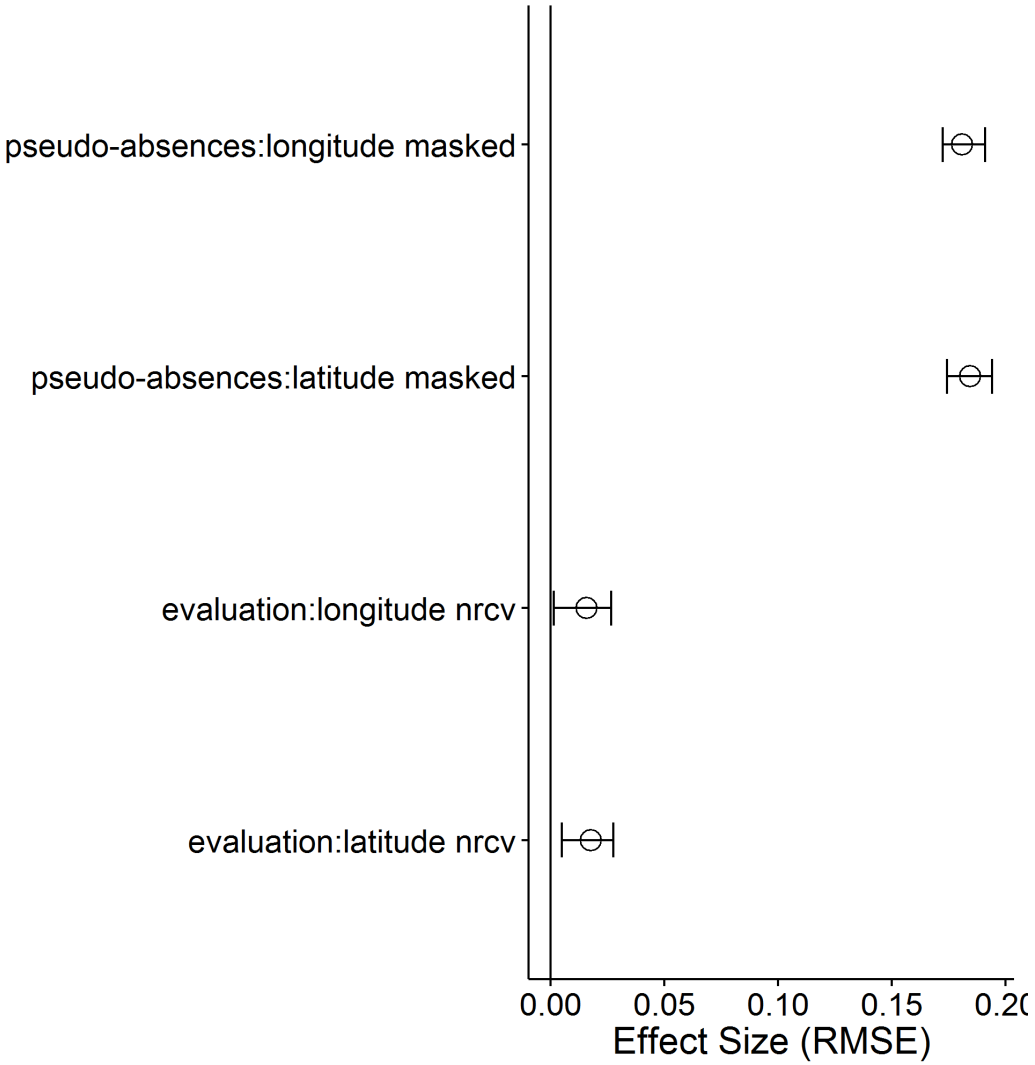


Figure 5.2 Coefficient estimates (effect size) for the fixed effects with parametric bootstrap 95% confidence intervals from the linear mixed effects model. The response variable was model performance (Root-mean square error, RMSE) and the fixed effects were pseudo-absence, evaluation and modelling techniques. Only the fixed effects pseudo-absence and evaluation method are shown here as they were the effects of interest. The effect sizes are compared to a reference, which was the non-masked pseudo-absence technique and the random cross-validation evaluation technique. Confidence intervals that do not include zero indicate a significant difference from the reference. Abbreviations are nrcv (non-random cross-validation).

With respect to the evaluation technique, non-random cross-validation also resulted in a significant decrease in model performance (i.e. increase in RMSE) in relation to random cross-validation (Figure 5.2). This result indicates that model performance may be overestimated (*i.e.* RMSE may be underestimated) due to the increased dependence of calibration and test datasets in random cross-validation. Consistent with the pseudo-absence results, both the longitudinal and latitudinal non-random cross-validation resulted in a similar increase of RMSE.

5.3.2 Extrapolation detection among evaluation techniques

To check whether the observed decrease of model performance was related to models having to extrapolate predictions, the distance between calibration and test datasets generated by the two evaluation methods (random and non-random cross-validation) was measured. The final linear mixed effect model to explain distance between calibration-test datasets included evaluation method as fixed effect and only species as random effect because adding genus and family resulted in higher AIC values (Table 5.2).

The mean distance (Exdet) between calibration-test datasets [95% CI] for random cross-validation was 0.069 [0.057- 0.081]. This range of values indicates that the test datasets generated by random cross-validation are environmentally similar to the calibration data, and thus, predominantly predictions were not extrapolated. Non-random cross-validation resulted in a significant decrease of distance in comparison to random cross-validation (Figure 5.3). Mean distance for non-random cross-validation is therefore closer to zero than mean distance for random cross-validation. This result indicates that spatially structuring datasets did not result in model extrapolation. Interestingly, latitudinal non-random cross validation created test datasets that were more similar to the calibration dataset than longitudinal non-random cross-validation

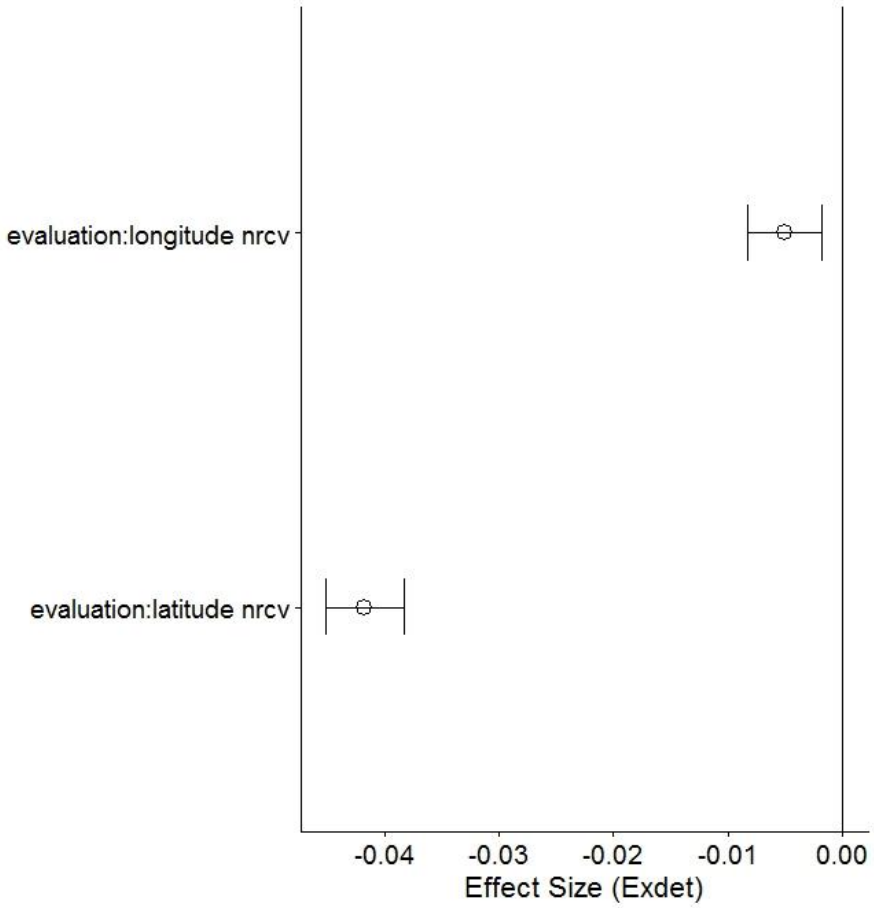


Figure 5.3 Coefficient estimates (effect size) for the fixed effect variables with parametric bootstrap 95% confidence interval from the linear mixed model. The response variable was the distance between calibration-test datasets measured by Exdet. The fixed effect was evaluation techniques. The effect sizes are compared to a reference, which was random cross-validation. The mean Exdet and 95% CI for the reference random cross-validation was 0.069 [0.057- 0.081]. Confidence intervals not including zero indicate a significant difference from the reference. Abbreviations are nrcv (non-random cross-validation) and Exdet (extrapolation detection).

When pseudo-absence generation and evaluation method were combined, masked non-random cross-validation resulted in the poorest model performance (*i.e.* highest RMSE), whereas non-masked random cross-validation resulted in the highest performance (*i.e.* lowest RMSE) (Figure 5.4).

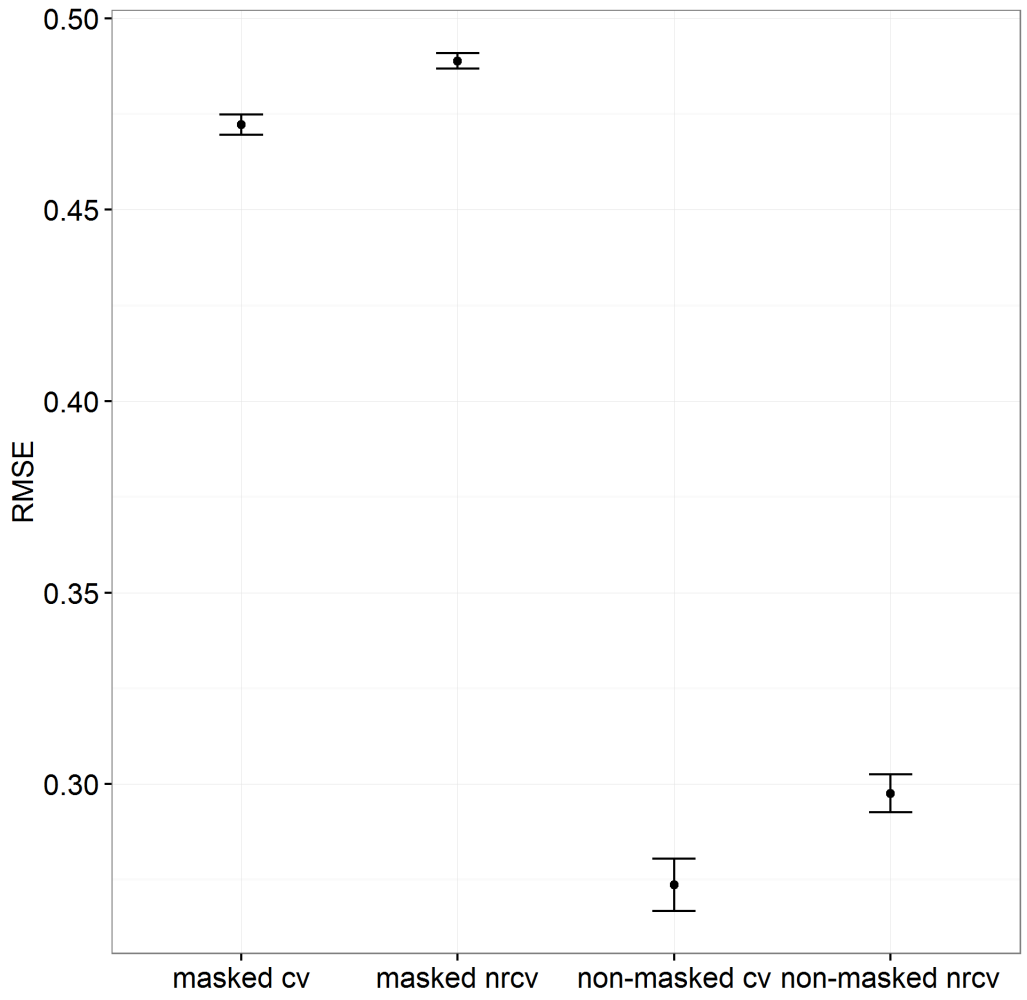


Figure 5.4 Influence of pseudo-absence generation and evaluation method on model performance. Average RMSE (root mean square error) over the nine models and 14 species are shown with the standard error bars. Non-masked pseudo-absence generation involves using the whole geographic background, whereas masked involves using just part of the geographic background. cv (random cross-validation) involves dividing the dataset randomly whereas nrcv (non-random cross-validation) the dataset is divided using longitudinal or latitudinal subsets.

5.3.3 Model transferability

When using random cross validation, differences in performance among models were evident (Figure 5.5). SVM and KNN had the highest performance (*i.e.* lowest RMSE) followed by NNET, QDA, CART and CTREE. Clearly these models outperformed NB, LOG and LDA. However, by splitting the evaluation datasets non-randomly, the difference in performance among the various modelling techniques diminished (Figure 5.5). Overall, there was a significant decrease in performance (*i.e.* increase of RMSE) when non-randomly splitting evaluation datasets for all models, particularly for SVM and KNN. All modelling techniques showed poor transferability because they all had difficulty predicting the independent datasets generated by non-random cross validation (indicated by high RMSE).

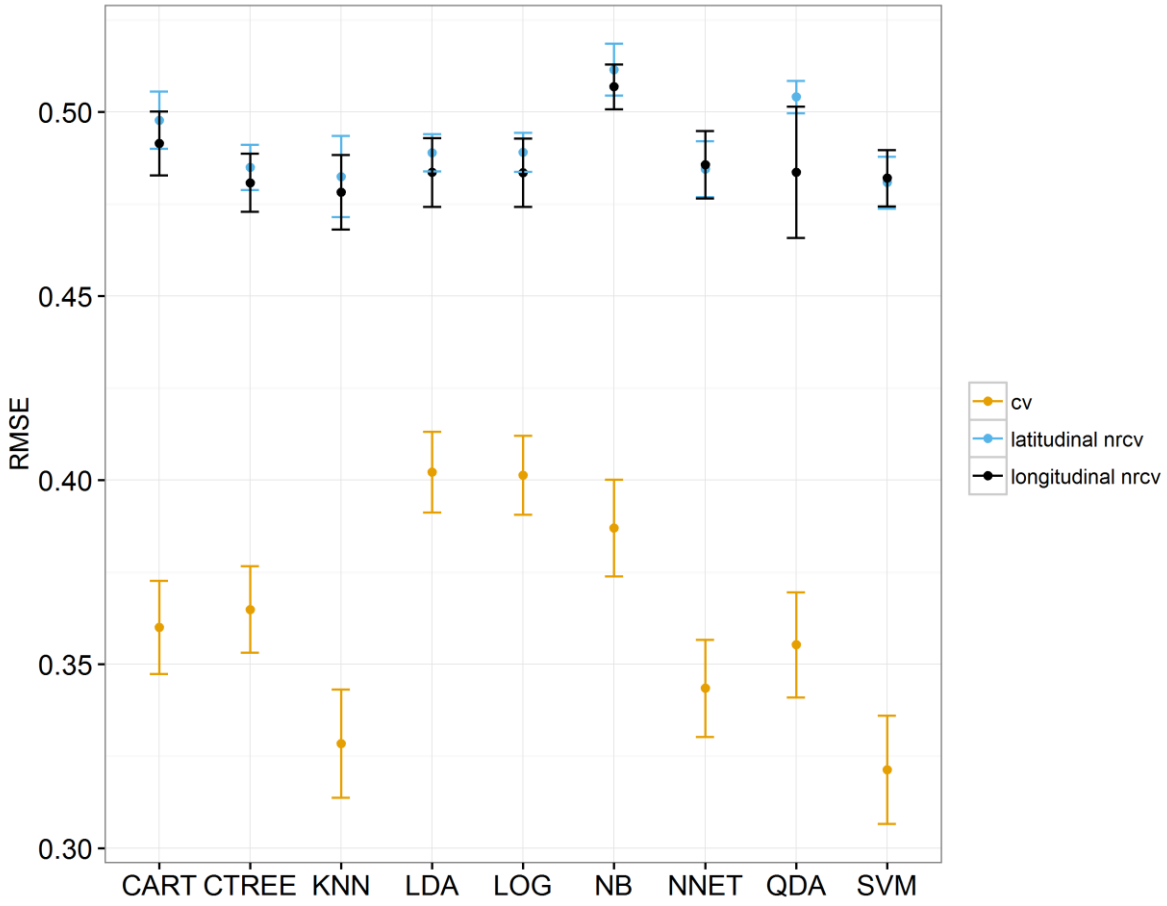


Figure 5.5 Model performance across the different evaluation methods for the nine SDM. Average RMSE (Root Mean Square Error) across the pseudo-absence generation methods and 14 species are shown with the standard error bars. cv (random cross-validation) involves dividing the dataset randomly whereas nrcv (non-random cross-validation) the dataset is divided using longitudinal or latitudinal subsets.

5.4 Discussion

This study confirmed the dependence between the calibration and test dataset that can arise from the conventional random cross-validation. More importantly, the research demonstrated for the first time the pitfalls of pseudo-absences generated by environmental profiling in the evaluation of model performance. I demonstrated that absences generated across the whole geographic background, can generate a dependence between the calibration and test datasets that resulted in a misleading estimation model performance. Accordingly, this work can be used to propose a framework for obtaining a more rigorous evaluation of model performance.

By masking the geographic background to generate pseudo-absences, model performance decreased (RMSE increased) in comparison to the non-masked pseudo-absence generation method (Figure 5.2). As I predicted, using presences from the whole geographic background to generate pseudo-absences, can introduce a bias by creating a dependence between the calibration and test datasets. By using the information across the whole geographic background to generate pseudo-

absences, information on the presences from the calibration dataset was introduced into the test dataset (through the generated pseudo-absences), which resulted in an inflated model performance. However, by masking parts of the geographic background, one ensures that no information from the calibration dataset is introduced into the test dataset.

The decrease in performance when using more independent datasets (non-random cross-validation), confirms the existing dependence between the calibration and test datasets generated by random cross-validation (Figure 5.2). This result is supported by other findings in the literature. In a case study of brook trout and brown trout, Wenger & Olden (2012) showed that three different models (random forests, generalized linear model and artificial neural network) indicated that an overestimated AUC which was correctly estimated with non-random cross validation. Similarly, in an assessment of model transferability, Bahn & McGill (2013) use the distributions of 79 bird species and four modelling techniques to assess the impact of dependence between the calibration and test dataset. Using different numbers of folds, they also showed that model performance decreased as calibration and tests datasets were more spatially segregated.

The combination of pseudo-absence and model evaluation technique indicated that masked non-random cross validation yielded the lowest model performance (Figure 5.5). This outcome is contrary to other studies which have suggested that masked non-random cross validation provided better performance than solely non-random cross validation (Radosavljevic & Anderson, 2014). However, the use of different pseudo-absence methods may explain this difference. In their study, Radosavljevic & Anderson (2014) modelled the distribution of *Heteromys anomalus* (Caribbean spiny pocket mouse) using Maxent. For this model, pseudo-absences are randomly selected from the geographic background, whereas in the current study, an environmental profiling technique was used (OCSVM), which involves using information from the presences. Thus, the random selection of pseudo-absences is not necessarily expected to create a strong dependence between calibration and test datasets as no information on the presences is used, which would explain the good performance found by Radosavljevic & Anderson (2014) for masked non-random cross-validation. Indeed this result highlights the importance of masking the geographic background to rigorously assess performance, particularly for absences generated by environmental profiling.

Nevertheless, it is important to discuss other factors that could alternatively explain the decrease of performance when spatially structuring the datasets. First, the fact that different sets of variables were used to predict each species dataset of presences and pseudo-absences, may have affected the evaluation of model performance. The way that the geographic background is used (non-masked, latitudinal and longitudinal masked) will result in a different set of pseudo-absences being generated for each species. Therefore, the variable selection procedure resulted in different

variables being selected for each species depending on the pseudo-absence generation method (Appendix C.1). Whether or not different variables used in the modelling framework negatively affected model performance is unclear. However, during variable selection using random forest, the least important variables are eliminated, in other words, the ones resulting in the lowest misclassification error when the values of the variable in a node are randomly permuted (Díaz-Uriarte & Alvarez de Andrés, 2006). Thus it is expected that variables selected for each dataset are optimal for the prediction of dataset, therefore the fact that different sets of variables were used shouldn't have negatively affected model performance.

Second, the alternative method non-random cross-validation was suspected to suffer from the problem of extrapolation which could explain the detected decrease in model performance in comparison to random cross-validation (Bahn & McGill, 2013). However, the analysis of the distance of calibration-test datasets suggest that most of the predictions were not extrapolated (Figure 5.3). This result indicates that the measured performance by spatially structuring the datasets could not have been affected by extrapolation. In fact, spatially-structured datasets created test datasets that were more similar to the calibration datasets than non-structured datasets. Interestingly, structured datasets based on latitude generated more similarity among calibration-test datasets than longitude subsets. That similarity could be due to the fact that there generally are more environmental patterns along latitudes than longitudes. For example, the Köppen-Geiger classification, which takes into consideration vegetation and climate patterns, clearly highlights an overall structure across latitudes, although in some areas some longitudinal patterns can be seen as well (Kriticos et al., 2012).

Third, another possibility that could explain the decrease of model performance in relation to random-cross-validation is spatial non-stationarity (Osborne & Suárez-Seoane, 2002; Bahn & McGill, 2013). This occurs when the relationship between species' distributions and environmental variables changes across space. Indeed, the importance of some variables for determining species' ranges may change depending on the particular part of the study region. For instance, Hothorn et al. (2011) found that altitude had a positive effect on the distribution of the red kite (*Milvus milvus)* in the western and north-western part of Bavaria whereas in other parts it had a negative effect. Thus, in this case, a model where altitude is considered to have the same effect across the range would have resulted in erroneous predictions of *M. milvus* distribution. Further research is needed to determine the presence of spatial non-stationarity in the proposed evaluation framework and whether it has affected the assessment of performance. The inclusion of non-stationarity in species distribution models is relatively recent (Miller, 2012) and tools that characterize and account for non-stationarity are emerging rapidly so that such ecological complexities can be accounted for (Mellin et al., 2014).

Even with the potential constraints of non-stationarity, I advocate the use of non-random cross-validation as an important additional test for model evaluation. Model transferability can only be determined with validity based on an independent dataset that, according to this research, can be best achieved by spatially structuring the data. The comparison of different strategies to generate independent datasets suggests that either longitudinal or latitudinal structuring work similarly (Figure 5.2). Despite these promising results, a direct assessment of the generated degree of independence between calibration and tests datasets, will confirm the validity of the proposed framework.

Moreover, in this study, conventional cross-validation indicated that some models such as SVM and KNN performed better than others (Figure 5.5). However, a dramatic decrease in performance occurred for all the models when independent datasets, such as those generated by non-random cross-validation, were used. Such a result suggests that the nine models show poor transferability to predict species' distributions. Other studies have found that complex models tend to show poor transferability. For example, Wenger & Olden (2012) established that NNET and random forests, that are considered more complex modelling techniques, had poor transferability in comparison to a generalized linear model. However, in the current study, both complex and simple models resulted in poor transferability, although some models, such as SVM and KNN, resulted in a stronger drop in performance when using spatially-structured data indicating that these models may tend to overfit more than the other models. Previous work in this thesis has demonstrated that these models often provide complex response curves, indicating potential data overfitting (Chapter 4). However, different strategies exist that could help to reduce overfitting such as adding a regularization term that penalizes model complexity or by controlling model parameters to reduce complexity (Merow et al., 2014). Transferability may have been affected also because the variables used for modelling may only have an indirect effect on the species (Wenger & Olden, 2012). For example, Sundblad et al. (2009) found that the use of salinity, which has a direct influence on the larval distribution of the fish roach (*Rutilus rutilus L.*), resulted in better transferability than the model built for a different species for which this variable had less effect. In a more general framework, based on 50 plant species, Petitpierre et al. (2016) investigated the importance of proximal variables, in other words, variables that have a direct impact in species physiological limits, on model transferability. Petitpierre et al. (2016) showed that model transferability was improved when variables with direct effects were used.

5.5 Conclusion

This study showed the impact of different pseudo-absence generation and evaluation methods on model performance. Performance was found to be inflated when pseudo-absences were generated

across the whole background and when conventional cross-validation was used. For rigorous model evaluation, pseudo-absences should be generated by masking the geographic background, particularly for environmental profiling techniques, to avoid any influence in the evaluation process. Moreover, models should be evaluated by spatially structuring the dataset to ensure independence between the calibration and test dataset. Such spatial stratification can be obtained by dividing the data either into longitudinal or latitudinal subsets. All the models used in this study showed poor transferability for the fourteen case study species. Consequently, predictions into new regions or at different times for these species should be interpreted with care.

Chapter 6

General discussion

In this chapter, I provide an overview of the objectives set in this thesis and discuss the major outcomes from the research. The limitations of this research are considered along with recommendations and suggestions for future research.

6.1 Niche conservatim and climatic equilibrium, examining key assumptions of species distribution models

A major aim of this thesis was to investigate the implications of the assumptions frequently made while using species distribution models (SDM) to determine the risk of invasive species establishment. To address this aim, the consequences of, and the opportunities generated by these assumptions were investigated in Chapter 2 and 3 and are further discussed here in a wider context.

A key assumption of the use of species distribution models is that species conserve their niche across space and time, also known as the niche conservatism assumption. Thus the first objective of this research was to test the generality of niche conservatism in freshwater ecosystems by describing and analyzing the climatic niche of 22 invasive freshwater invertebrates during the process of invasion (Chapter 2). Most of the species studied in this thesis (90%), exhibited a niche shift, suggesting that they are able to colonize different environments than the ones observed in their native range. This study provided for the first time a general overview of the frequency of niche conservatism in freshwater invertebrates, and contrary to other organisms, I showed that niche shifts are more the rule rather than the exception. For example, using the invasion of the Mediterranean by 30 marine fish, Parravicini et al., (2015) found that for 33% of these species, their niche had shifted. Also for birds, Strubbe et al. (2013) demonstrated that of the 28 invasive birds in Europe, only 29% species showed a niche shift. On the other hand, Petitpierre et al. (2012) found a much more conservative degree of niche shift for plants, where only 14% of 50 terrestrial invasive plants exhibited a niche shift.

Petitpierre et al. (2012) stated that the high degree of niche conservatism in plants supports the use of SDM for the prediction of both biological invasions and effects of climate change in species distributions. However, the research in this thesis showed that for freshwater invertebrates, the use of SDM may result in an underestimation of their potential invasion if niche shifts are not accounted for, highlighting the existing challenges for invasion mitigation in freshwater ecosystems. Indeed, Broennimann & Guisan (2008) recommended to use both native and invaded distributions to account for existing niche shifts. This recommendation can be of particular importance for invasive species

risk assessment, where frequently only the native range is considered to determine whether the focal species can establish in an the area of interest (Kumschick & Richardson, 2013). To assess the effect of lack of niche conservatism in predictions, I assessed whether the degree niche shift can negatively affect model performance. In contrast to other studies (Petitpierre et al., 2012; Strubbe et al., 2013), no significant evidence was found for a relationship between niche conservatism and model performance probably because using information on both the native and invasive distributions to implement SDM already accounted for the detected niche changes. Nevertheless the challenge still lies in accounting for niche shifts when there is a lack of information on the distribution in the invaded range.

To use SDM, it is also presumed that species occupy all the suitable environments in their distribution, in other words, species are in equilibrium with their environment. There is considerable evidence showing that most species are not in equilibrium with their environment (Araújo & Pearson, 2005; De Marco et al., 2008). So far, however, there has been little discussion on when and at which rate species can reach equilibrium. Therefore, the second major objective of this thesis was to determine if there was a significant effect of residence time on species' niche dynamics and to determine the necessary time for invasive freshwater invertebrates to reach an equilibrium. Using a set of nine invasive freshwater invertebrates, I showed that their invasive niche progressively filled with increasing residence time, which confirms the limitations of the equilibrium assumption. More interestingly, this research determined that on average, invasive freshwater invertebrates required 122 years to reach equilibrium which is faster than other organisms, such as plants which Williamson et al. (2009) estimated to require 150 years. In this study, I proposed to quantify the time to equilibrium by characterizing climatic disequilibrium instead of range disequilibrium as in other studies (Pyšek & Prach, 1995; Williamson et al., 2009). A range disequilibrium, is where a species has not filled its potential geographic space. A range equilibrium does not necessarily result in a climatic disequilibrium, as species may have already filled their climatic niche. Therefore, measuring a climatic disequilibrium will better anticipate the validity of using SDM to determine the potential distribution in the invaded range.

By examining the niche dynamics across time by using earlier records of invasion, I also demonstrated that species tended to colonize new environments not previously occupied in the native range (Chapter 3). These results emphasize that SDM calibrated at early stages of invasion, using only native range information, will tend to underestimate their potential distribution. Based on these analyses, it is clear that correlative SDM need to be constantly updated in recognition of potentially limiting assumptions.

In both Chapters 2 and 3, the research clearly illustrated the importance of considering niche dynamics for risk assessment, surveillance and management. First, the study of niche dynamics during invasion, facilitates the identification of species that may have particular abilities to colonize new environments. While the mechanism behind any niche shift indicated by such analyses needs to be investigated; the assessment of niche shifts can indicate species that are of potential concern. This information will be extremely useful for invasive species risk assessment especially to assess the likely area of impact that a species could have as well as to identify species with potential for rapid spread. In Chapter 3, analyses were developed for improved identification of rapid spreaders or species undergoing a lag phase in their invasion that could further provide an indication for risk assessors of their potential impact and possible control or management strategies. Second, I showed that niche information can be used to identify areas of high risk of invasion. In Chapter 2, a novel approach of combining climate suitability and niche stability information was demonstrated, where hotspots of invasion around New Zealand were identified for 19 invasive freshwater invertebrates. By characterizing environments throughout New Zealand similar to those where each species showed niche stability, areas of higher risk of invasion were identified. As a result, surveillance can be prioritized within these areas.

More recently, the implications of niche dynamics for conservation has been highlighted, demonstrating how this research could be extended to achieve conservation benefits. For instance, Breiner et al. (2017) showed that changes in niche size provided additional information on the simulated extinction events of vascular plant species. As result, they advocate the use of niche dynamics to complement the traditional use of range size change in the IUCN Red list assessments of potential for extinction. Correspondingly, an analysis of niche dynamics and potential changes in niche size should be standard practice in conservation, and particularly, for invasive species risk assessment to provide useful insights on species invasiveness that may shed light on opportunities to monitor, control, and, particularly the potential to eradicate such species.

6.2 Challenges with respect to model transferability

One of the most desirable characteristics for predictive modelling using SDM, is model transferability. Fully transferable models are able to generalize a species' niche and, therefore, predictions of such models of the potential establishment for new areas and/or different times are considered more reliable. The major problem that affects model transferability is when predictions are made outside of the calibration range, in other words, when predictions are extrapolated. Several authors warned against extrapolation because of the high uncertainty expected in predictions and the lack of knowledge to validate those predictions (Fitzpatrick & Hargrove, 2009; Kriticos et al., 2013; Guisan et al., 2014). However, a thorough evaluation was required to fully evaluate the above-mentioned

claims. Therefore the third objective of this thesis was to compare the uncertainty associated with extrapolated and interpolated predictions. When the predictive uncertainty for 21 invasive freshwater species was measured interpolated and extrapolated predictions over a global extent, the results showed that extrapolated predictions, as expected, resulted in higher uncertainty. However, the predictive uncertainty of interpolated predictions was also found to be extremely high suggesting that using some interpolated predictions may also be problematic. Surprisingly, the models performed similarly, yet they related species responses to environmental variables very differently (Chapter 4). Clearly, current measures to evaluate performance provide a general overview of model performance but do not characterize where the errors might occur.

Since extrapolation in some circumstances is necessary, the third objective was to identify models that provided ecologically plausible species response curves under extrapolation. However, species response curves for the same variables differed greatly among models, such that, it was challenging to identify which models provided the most plausible relationships. Despite this result, a deeper understanding of how the models characterized species response was gained. In some circumstances, some models, such as artificial neural networks, k-nearest neighbours, conditional trees and support vector machines, provided overly-complex responses which contained several inflections and turning points. In contrast, logistic regression, naïve Bayes, linear discriminant analysis and quadratic discriminant analysis, provided a range of simpler, smoothed curves. This brings up the ongoing debate on the degree of complexity that should be used in predictive ecology (Evans et al., 2013; Merow et al., 2014).

In a significant review on the topic of complexity, Merow et al. (2014), argued that the amount of complexity in a model should be decided based on the objective of the study and the type of data available. For example, there will be a difference if the objective of the study is to describe the niche or for range mapping a species, compared with an objective to test a hypothesis or to generate one. Moreover, Merow et al. (2014) suggests that the important features of the data that should be considered include: sample size, sampling bias, type of predictors used, the spatial extent and resolution and the degree of spatial autocorrelation. Complex models will describe the data without imposing any assumption on the relationship of the species response to the environmental variables. Therefore, complex models are useful to generate hypothesis on novel responses. In contrast, simple models can test whether the data meet an ecological hypothesis concerning the species response. In general, there is no clear agreement on the particular shape that a particular species response should have in relation to key variables. For instance, evidence of bell shape curves, which represent the suitability to the environment dropping when moving away from an optimum, is scarce (Austin, 2002). Thus, based in the research in this thesis, I propose that combining complex and simple modelling approaches can provide useful insights on species distributions. Instead of combining the

predictions across models, I recommend the use of an appropriate ensemble method that identifies models with similar assumptions to showcase different scenarios of the risk of establishment of invasive species.

The challenge remains to identify complex and simple models that are able to best characterize the species response without overfitting or underfitting the relationship. Only by performing a rigorous model evaluation and therefore validating models, can predictions can be used across different times and space. Accordingly, the fourth objective of this thesis was to identify models that are able to generalize (or transfer) to new conditions. Unfortunately, the most widespread evaluation method, random cross-validation, suffers from the effect of dependence between the calibration and test datasets resulting from occurrence points being spatially autocorrelated (Wenger & Olden, 2012; Bahn & McGill, 2013). This method is considered likely to result in selecting models that overfit the data and are thus, not able to generalize species distributions. This research confirmed the effect of this dependence on model performance, which is shown by the measured high performance when using random cross-validation compared to when a more independent test dataset was used (non-random cross-validation). But more importantly, I demonstrated that the dependence between the calibration and test datasets can be exacerbated when pseudo-absences are generated across the whole geographic background. The effect of pseudo-absences generation on the assessment of model performance has received much less attention in the literature. To my knowledge, only Radosavljevic & Anderson (2014) have attempted to address this issue, however their recommendations apply to randomly generated pseudo-absences. In this study, pseudo-absences were generated using presence information (environmental profiling) and accordingly I provided a protocol to reduce the dependence for those type of absences. By spatially structuring the data into longitudinal and latitudinal subsets and then masking the geographic background using these subsets to generate pseudo-absences, one can ensure that only presences from the corresponding subsets will be used to generate pseudo-absences. Thereby more independence between the calibration and test datasets can be achieved. Thus, it is expected that by using this framework a more realistic estimation of model performance is obtained.

Using the proposed evaluation framework, I showed that all models indicated poor transferability for predicting the distribution of invasive freshwater invertebrates. Some models appear to overfit the data, particularly support vector machines and k-nearest neighbours, which both showed a large decrease in model performance when using more independent test datasets generated by non-random cross-validation. This result highlights the importance of controlling model complexity. In this context, regularization terms or controlling model parameters during model implementation will reduce overfitting and should be further investigated to confirm whether overfitting actually occurs. More importantly, however, the poor transferability detected in this study

could be the result of using distal variables which do not directly affect species distribution but have an indirect effect though their relationship to important variables. Further discussion about this point can be found in the section 'Research limitations'.

I proposed the evaluation framework for SDM with the assumption that by spatially structuring the dataset, the dependence between the calibration and test datasets is reduced. However, a direct assessment of the degree of the dependence would shed light on the effectiveness of the proposed framework. Also, the conservative measure of model performance found in this framework may be the result of the effects of other methodological problems such as different sets of variables used to predict the species distribution, extrapolation and spatial non-stationarity. Because different sets of pseudo-absences were generated for each method (non-masked, latitudinal and longitudinal masked datasets), this resulted in a selection of different variables to predict the different datasets of presence and pseudo-absences. However, I expect that the use of different variables to predict different datasets shouldn't negatively affect the performance of the models as the methodology used to select variables (random forests) is optimized to select variables that are important for predicting the set of presence and pseudo-absences. Furthermore, an effect of extrapolation on the proposed framework is unlikely, as I found that when datasets were spatially structured, most of the predictions were not extrapolated. With respect to spatial non-stationarity, in other words, when the importance of some variables for determining species distribution change across space, further research is needed to determine the presence of non-stationarity in spatially structured datasets and whether it has impacted the assessment of performance.

6.3 The risk to New Zealand from invasive freshwater invertebrates

In this work, New Zealand was used as case study to showcase the challenges associated with using correlative species distributions models to predict the potential for invasion of selected freshwater invertebrates. In Chapter 2, several areas in New Zealand were identified to be particularly at risk of invasion by freshwater invertebrates. However, because predictions in novel areas come with several challenges, such as predictions in areas where the models potentially extrapolated, I assessed how frequently predictions were extrapolated for the 21 invasive freshwater invertebrates (Chapter 4). Most of the predictions in New Zealand were inferred by interpolation, although both univariate and multivariate extrapolation were detected as well. Some authors recommend that a map of uncertainty be provided for assessment, by representing specific areas where extrapolation has occurred (Fitzpatrick & Hargrove, 2009; Elith et al., 2010; Owens et al., 2013). However in this study, I found high uncertainty for both extrapolated and interpolated predictions and therefore more cautious consideration is needed if such maps are used to highlight uncertainty in predictions. Therefore, to improve the assessment of uncertainty in predictions, I recommend to interpret maps

of extrapolation with associated maps of predictive uncertainty to identify specific locations where models show high uncertainty.

Predictions in novel areas also require models that reliably transfer predictions. The framework developed in Chapter 5 to rigorously test model transferability, indicated that the nine models used are limited for predicting freshwater species distributions into new areas. The limitations detected, based on the models used, make the predictions generated in this study uncertain for making surveillance or policy-related decisions regarding the potential invasion of freshwater invertebrates. The general inability of these models to reliably predict the distribution of freshwater invertebrates assessed in this study, is likely based on the limits of our knowledge of species' niche (see "Research limitations" for further discussion).

However, despite the limited transferability for the species studied here that does not exclude that under certain circumstances, some models might be able to show a reasonable transferability for individual species. Uncertainty is an inevitable component of any modelling framework and therefore determining what levels of uncertainty are acceptable for making decisions requires future consideration.

6.4 Research limitations

Throughout this work, limitations were recognized that potentially had an impact on model outcomes. It is well recognized that climatic variables were used in this study as a proxy to characterize freshwater species' niches, and that such variables may have influenced the detection of niche shifts and also may have affected the assessment of model transferability. Indeed, some studies have shown that niche shifts are more common when variables that have low impact on species distribution are used. For example, using birds as a case study, Strubbe & Matthysen (2014) found, that niche shifts were more common among variables having a localized impact on the species distribution. Other non-climatic factors, such as freshwater variables and anthropogenic influence clearly need to be examined, but separately from macroclimate factors, to assess their relative effect on the detection of niche shifts (Guisan et al., 2014).

In addition, when investigating model behaviour in response to specific variables, I found that some models gave flat trends for certain variables indicating that those variables may not necessarily have a strong influence on the particular species occurrence. Indeed, Elith & Graham (2009) used a virtual species to examine the ability of models to characterize the simulated species response to several environmental variables. They found that environmental variables that had a high contribution to the response were better characterized by the models. In the current study, not all models characterized flat trends for the same variable, indicating that either some models were

weighting variables differently (Capinha et al., 2011) or were able to characterize weak trends. If the observed flat trends are related to variables having a weak influence on species distribution predictions, then this might have affected model transferability. Correspondingly, Petitpierre et al. (2016) found that model transferability improved when variables with a direct impact on species distributions were used. In Chapter 5, I found that all models had poor transferability when predicting freshwater invertebrates distribution (Chapter 5), potentially because some of the variables used had a limited impact on species distribution.

The climatic variables used in this study reflect the average, extremes and seasonality of hydrothermal conditions. Most of these predictors are distal variables, in other words, variables that indirectly, affect species distributions by being related to more proximal variables (Austin, 2002; Merow et al., 2014). For instance, air temperature is a distal variable that is correlated with water temperature, which directly constrains freshwater species distributions (Chapter 1). However, the main difficulty of using distal variables is that correlation with proximal variables can change across space and this will undermine the estimation of probability of occurrence (Dormann et al., 2013; Merow et al., 2014). Further work is required to assess under which circumstances distal variables are able to provide reliable predictions, by determining, for example, where the correlation to proximal variables significantly changes. This could be achieved at regional scales in some areas of the world, where proximal variables are available for modelling (e.g., Chee & Elith (2012), https://teamwork.niwa.co.nz)

To successfully model freshwater species distributions at global scale, freshwater environmental data is needed. In a recent effort, Domisch et al. (2015) generated a database that takes into account stream connectivity and consequently enables upstream environmental conditions to be traced back, which can facilitate much improved modelling in freshwater ecosystems. However, this database still only considers distal variables such as climate (air temperature), topography and landcover to name a few. There are currently hydrological models that can predict flood, droughts and river discharge (Wang et al., 2011), but these models come with the same uncertainties associated with any model, and there are challenges of modelling such variables at a global scale as they require high-resolution meteorological input data. The development of freshwater-related predictors such as water temperature, stream runoff and flood regimes at a global scale will greatly advance species distribution modelling.

6.5 Future work

6.5.1 Which mechanisms underlie the detected niche shifts?

In Chapter 2, it was found that most of the selected freshwater invertebrates, have undergone a niche shift in their invaded range. Identifying the mechanisms behind these shifts will increase our understanding of the success of these invasions. Ecological responses, such as release from dispersal constraints, biotic interactions and/or evolutionary processes or a mixture of all of these are possible explanations of these niche shifts (Alexander & Edwards, 2010). For instance, the New Zealand snail, *Potamopyrgus antipodarum* (Gray 1843, Tateidae) is an island endemic species that may have been able to colonize novel environments in their invasive range due to pre-adaptation. However, this species success may also be related to a release from parasitic trematodes, which are found in higher incidence in the native range (Alonso & Castro-Díez, 2012). A multidisciplinary approach, such as the one used by Rey et al. (2012), may be able to unravel the actual mechanisms underlying niche shifts. In their study, Rey et al. (2012) investigated whether adaptation occurred during the invasion in Israel by the tropical ant *Wasmannia auropunctata* (Roger 1863, Myrmicinae) by increasing physiological tolerance to cold climates. First, by using SDM, they identified areas similar to the invaded range, to find ant populations that potentially were under cold temperature selective pressure. Once these populations were sampled, they conducted a genetic analysis to determine the origin of the populations that were able to establish in Israel. Then experiments on temperature tolerance were undertaken on several ant populations to determine if an actual adaptation occurred. Their study showed that prior-adaptation occurred at cold climates in the native range before dispersal to Israel. A similar framework could be applied for a selection of invasive freshwater species from this study to disentangle the mechanism responsible for the detected niche shifts.

6.5.2 Which factors can predict niche shifts?

Niche shifts are usually detected once a species has invaded a new area. Thus, it will be useful to identify key factors that will predict the likelihood of species going through a niche shift. Species-related characteristics, and, biogeographical and habitat factors are believed to be associated with the ability of species to occupy new environments (Capinha & Pateiro-López, 2014; Byers et al., 2015; Liu et al., 2017). For instance, life history strategies and phenotypic plasticity related traits were investigated by Capinha et al. (2014), to explain the ability of terrestrial gastropods to occupy novel environments using egg volume, maximum shell length, presence of a protective shell, polymorphism shell colour and reproductive strategy. Likewise, Liu et al. (2017) used body size and clutch size as a proxy for dispersal capabilities for herpetofaunal species. Biogeographical factors, such as species' origins (island endemics) or the native niche breath could explain the likelihood of niche shifts due to dispersal constraints. In this study, residence time was identified as factor explaining changes in the

invasive niche (Chapter 3). Thus, this factor could be also used to determine the likelihood of a niche shift. Furthermore, information on the type of habitat in the native and invasive range may explain niche shifts caused by anthropogenically or environmental stress induced adaptation.

6.5.3 Investigating extrapolation behaviour of a model using virtual species

In Chapter 4, model behaviour was investigated under interpolation and extrapolation conditions. However, whether models provided ecologically plausible responses under extrapolation could not be determined. Using virtual species, one might be able to control the factors that are desired to be tested. In particular, more knowledge is needed to understand how models behave with varying features of the data (e.g., sampling bias, spatial autocorrelation and sample size) as well as how models characterize variables having different impact on species distribution. To generate a realistic virtual species, Naimi et al. (2014) proposed direct use of real species occurrence and environmental variables to generate distributions by implementing SDM. These predicted distributions can be assumed to be the 'true' distribution of the species. This method would enable the generation of a realistic virtual species under different assumptions such that simple and complex ecological responses can be investigated.

6.5.4 Directly correcting spatial autocorrelation in species occurrences

In Chapter 5, I identified the effect of spatially autocorrelated occurrences on the measurement of model performance and a framework was proposed to alleviate those effects on the model evaluation process. However, the effect of spatially autocorrelated occurrences on model predictions was not considered. The presence of spatial autocorrelation may result in biased parameter estimates (Bahn & McGill, 2013). Despite spatial filtering of species occurrences was applied to reduce spatial autocorrelation, it may not ensure complete removal of autocorrelation. In fact, the practice of geographical spatial filtering is widespread and there are R packages to perform different types of filtering (Hijmans et al., 2017). However, one could perform environmental filtering within the niche that retains only the occurrence points that show unique environmental characteristics. This procedure will ensure the removal of spatial autocorrelation directly in the environmental space and would guarantee a complete coverage of the species niche. Alternatively a study by Varela et al. (2014) proposes a simple environmental filtering using only a gradient of temperature and precipitation. Perhaps an appropriate clustering technique would also enable environmentally unique occurrences to be selected while considering numerous environmental dimensions.

6.6 Concluding remarks

Investigating the niche dynamics of the selected species in this research, generated opportunities to understand the process of invasion as well as to develop approaches to assist surveillance and

invasive species risk assessments. In this thesis, niche shifts were determined to be frequent in invasive freshwater invertebrates highlighting the challenges for anticipating their impact in freshwater ecosystems. Species of specific concern, particularly those with an ability to colonize new environments and spread very rapidly, were identified and consequently this type of information should be considered in invasive species risk assessments. The novel approach of using niche information and climate suitability developed in this work, helped identify areas of high risk of invasion and such knowledge can support the prioritization of surveillance areas and optimization of resources.

The high predictive uncertainty detected in this study, showed some limitations of the correlative species distribution models for transferring predictions of freshwater invertebrates to novel areas. This work has contributed to the development of rigorous methods to evaluate uncertainty and has showcased a range of tools that can assist decision-making about invasive species under uncertain scenarios. Significant gain in knowledge about predictive models was achieved by identifying different types of model behaviour that can provide different scenarios of predictions. The combination of various degrees of model complexity can provide useful insights about species responses to the environment and therefore reduce the uncertainty related to the modelling technique and quality of data. As Merow et al. (2014) perfectly summarized: “We are faced with the challenge of inferring unknown levels of ecological complexity through the lens of data and models that imperfectly capture it”. The difficulties associated with predicting species distributions will not be overcome by investigating each isolated component, but rather by understanding the species niche, the models used, and how they interact with each other, while acknowledging the limitations of the data.

Appendix A **Supplement chapter 2**

A.1 Centroid index description

The centroid index can be computed using the outputs of a Principal Component Analysis (PCA) from environmental characteristics of the native and invasive distributions. The function allows you to compute the index across all environments within the geographic background of the native and invasive range or only in analogous environments. The centroid index is computed as follows (Figure A 1):

- Centroids are located at the median of the points in the invasive and native distributions (for example black square and black triangle).
- The Euclidean distance is measured between the two centroids and it is divided by the distance that encompasses all points (distance between the two black stars)

An R script to compute this index is available in A.2

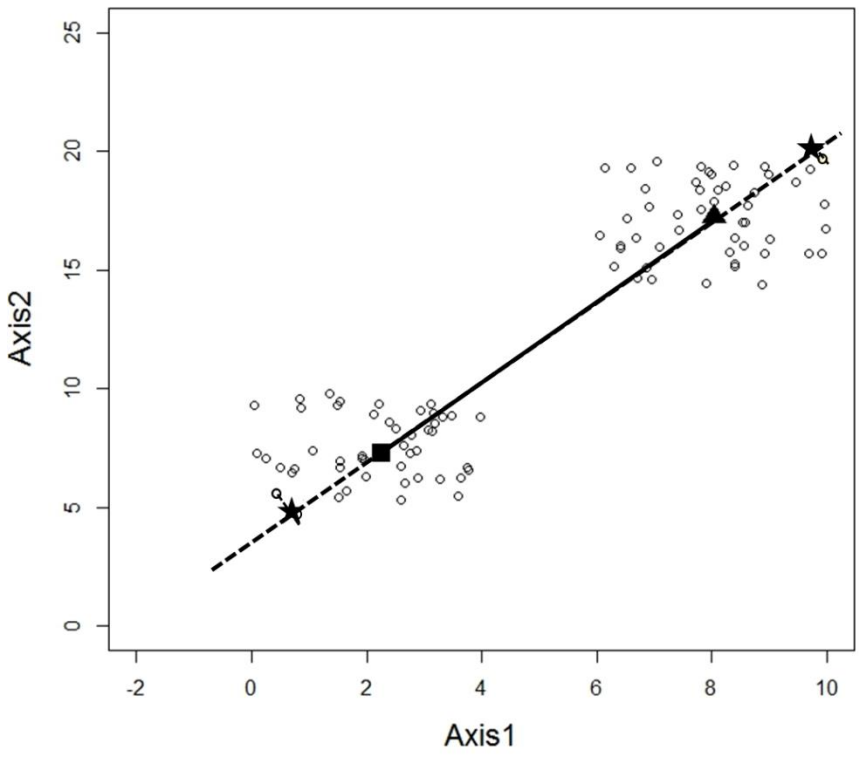


Figure A 1 Diagram illustrating how the centroid index is computed.

A.2 R script for the function centroid index

```
#Function for computing the centroid index
#Needs library raster
#Part of the code was extracted from function ecospat.niche.dyn.index
(library ecospat) to remove non analogous environments and marginal
environments
#scores.sp1 and scores.sp2  is a two column dataframe with the scores from
a PCA of native and invasive occurrence points
#If desired this index can be computed only in analogous environments, or
in the most common environments sensu Guisan et al 2014
#For this you need to provide the following arguments:
#z1 and z2 is a gridclim object created with function
ecospat.grid.clim.dyn. Theese objects are environmental grids for the
native and invasive range respectively
#scores.clim12 is a two column dataframe of the scores from a PCA of whole
study area (native+invasive backgrounds)
#intersection is the quantile of the environmental density used to remove
marginal environments (see function ecospat.niche.dyn.index from package
ecospat)
centroid_index<-function (scores.sp1,scores.sp2,z1=NA,
z2=NA,scores.clim12=NA,intersection =NA )
{
  if(!is.na(z1)|!is.na(z2)|is.na(scores.clim12))
 {
  w1 <- z1$w
  w2 <- z2$w
  glob1 <- z1$Z
  glob2 <- z2$Z
  if (!is.na(intersection)) {
    if (intersection == 0) {
      glob1[glob1 > 0] <- 1
      glob2[glob2 > 0] <- 1
    }
    else {
      quant.val <- quantile(glob1[glob1 > 0], probs = seq(0,
                                                          1,
intersection))[2]
      glob1[glob1[] <= quant.val] <- 0
      glob1[glob1[] > quant.val] <- 1
      quant.val <- quantile(glob2[glob2 > 0], probs = seq(0,
                                                          1,
intersection))[2]
      glob2[glob2[] <= quant.val] <- 0
      glob2[glob2[] > quant.val] <- 1
    }
    glob <- glob1 * glob2
    w1 <- z1$w * glob
    w2 <- z2$w * glob

    #cells that will help select occurrence points that will be used for
the centroid index
    w <- w1 + 2*w2
    w_inv<-t(w)[ncol(w):1,]

    #create grid
    xmin <- min(scores.clim12[, 1])
    xmax <- max(scores.clim12[, 1])
    ymin <- min(scores.clim12[, 2])
    ymax <- max(scores.clim12[, 2])
    raster_class<-raster(w_inv,xmn=xmin,xmx=xmax,ymn=ymin,ymx=ymax)
    #extract categories and remove points that are outside of selected
cells w
```

```
    scores.sp1$class<-extract(raster_class,scores.sp1)
    scores.sp2$class<-extract(raster_class,scores.sp2)

    scores.sp1<-scores.sp1[!scores.sp1$class==0,c(1,2)]
    scores.sp2<-scores.sp2[!scores.sp2$class==0,c(1,2)]
  }
}
  centroid1<-apply(scores.sp1,2,median)
  centroid2<-apply(scores.sp2,2,median)

  centroid<-rbind(centroid1,centroid2)

  #distance between two centroids
  dc1c2<-sqrt(1e-12+(centroid[2,1]-centroid[1,1])^2+(centroid[2,2]-
centroid[1,2])^2)#1e-12 so it can never be 0

  #unit vector connecting the centers
  u<-(c((centroid[2,1]-centroid[1,1]),(centroid[2,2]-centroid[1,2]))/dc1c2)

  #dot product with all points
  p<-as.matrix(rbind(scores.sp1,scores.sp2))%*%u

  #centroid index
  centroid_index1<-dc1c2/(max(p)-min(p))



  return(centroid_index1)

}
```

A.3 Variables selected by random forests for each species

Table A 1 Variables selected by random forests for each species.

Species name	Variable
Corbicula fluminea (O. F. Müller, 1774)	cbio01,cbio03,cbio04,cbio05,cbio07,cbio10,cbio14,cbio15,cbio17,cbio19,cbio21,cbio22,cbio23,cbio26
Pseudodiaptomus inopinus (Burckhardt, 1913)	cbio01,cbio02,cbio06,cbio11
Gammarus tigrinus (Sexton, 1939)	cbio01,cbio02,cbio07,cbio15,cbio21,cbio26
Aedes albopictus (Skuse, 1895)	cbio01,cbio02,cbio05,cbio06,cbio07,cbio08,cbio10,cbio11,cbio12,cbio13,cbio14,cbio15,cbio16,cbio17,cbio18,cbio19,cbio20,cbio21,cbio25,cbio26,cbio27
Hemimysis anomala (G.O. Sars, 1907)	cbio02,cbio06,cbio16,cbio18
Eriocheir sinensis (Milne-Edwards, 1854)	cbio01,cbio03,cbio04,cbio06,cbio07,cbio08,cbio09,cbio10,cbio11,cbio12,cbio14,cbio19,cbio25
Rhithropanopeus harrisii (Gould, 1841)	cbio01,cbio09,cbio11,cbio13
Valvata piscinalis (Muller, 1774)	cbio02,cbio04,cbio05,cbio07,cbio10,cbio20,cbio22,cbio23,cbio26,cbio27
Cercopagis pengoi (Ostroumov, 1891)	cbio01,cbio02,cbio03,cbio04,cbio06,cbio07,cbio11,cbio20
Bithynia tentaculata (Linnaeus, 1758)	cbio01,cbio02,cbio05,cbio06,cbio07,cbio09,cbio10,cbio11,cbio20,cbio21,cbio22,cbio23,cbio26,cbio27
Pomacea canaliculata (Lamarck, 1828)	cbio01,cbio05,cbio06,cbio7,cbio08,cbio09,cbio10,cbio11,cbio13,cbio19
Limnoperna fortunei (Dunker, 1857)	cbio05,cbio10,cbio12
Cipangopaludina japonica (von Martens, 1861)	cbio02,cbio10,cbio18

Dikerogammarus villosus (Sowinsky, 1894)	cbio01,cbio04,cbio06,cbio07,cbio11,cbio12,cbio18,cbio20,cbio22,cbio26,cbio27
Procambarus clarkii (Girard, 1852)	cbio01,cbio06,cbio11,cbio13,cbio22,cbio23,cbio27
Orconectes virilis (Hagen, 1870)	cbio04,cbio05,cbio07,cbio08,cbio09,cbio10,cbio12,cbio17,cbio18,cbio25
Dreissena rostriformis bugensis (Andrusov, 1897)	cbio02,cbio03,cbio04,cbio08,cbio14,cbio17,cbio19,cbio20,cbio24
Pacifastacus leniusculus (Dana, 1852)	cbio01,cbio04,cbio05,cbio06,cbio07,cbio10,cbio15,cbio22,cbio23,cbio27
Orconectes limosus (Rafinesque, 1817)	cbio01,cbio03,cbio04,cbio05,cbio10,cbio12,cbio20,cbio23,cbio27
Bythotrephes longimanus (Leydig, 1860)	cbio01,cbio03,cbio06,cbio09,cbio11,cbio18,cbio22,cbio23
Dreissena polymorpha (Pallas, 1771)	cbio01,cbio10,cbio12,cbio18,cbio20,cbio21,cbio26

A.4 Initial parameters tested for model parametrization

Table A 2 Parameters tested for model parametrization.

Model	Parameters	Initial values
KNN	k (number of neighbours)	4 to 20
SVM	kernel function	radial basis kernel
	C (cost of constraints violation)	0.1,1,10,100
	Sigma (inverse kernel width)	0.01,0.1,0.3,0.5,0.7,0.9
NNET	size (number of units in the hidden layer)	2,3,4,5
	maxiter (maximum number of iterations)	500,750,100,012,501,000
	weight decay	0.01,0.001,0.0001

A.5 Final model parameters used for KNN, SVM and NNET obtained by testing different set of parameters (A.4) using cross-validation.

Table A 3 Final model parameters used for KNN, SVM and NNET obtained by testing different sets of parameters (A.5) using cross-validation.

Model	KNN	SVM		NNET		
Species name	k	C	sigma	Size	Maxiter	Decay
Aedes albopictus (Skuse, 1895)	4	10	0.5	5	1500	0.01
Bithynia tentaculata (Linnaeus, 1758)	6	100	0.5	5	500	0.01
Bythotrephes longimanus (Leydig, 1860)	4	100	0.3	5	1000	0.01
Cercopagis pengoi (Ostroumov, 1891)	6	1	0.5	4	500	0.01
Cipangopaludina japonica (von Martens, 1861)	5	10	0.7	3	750	0.001
Corbicula fluminea (O. F. Müller, 1774)	4	10	0.9	5	500	0.01
Dikerogammarus villosus (Sowinsky, 1894)	7	10	0.3	3	1250	1.00E-04
Dreissena polymorpha (Pallas, 1771)	4	100	0.5	5	1000	0.01
Dreissena rostriformis bugensis (Andrusov, 1897)	5	100	0.5	5	1000	0.001
Eriocheir sinensis (Milne-Edwards, 1854)	4	100	0.5	5	1000	0.01
Gammarus tigrinus (Sexton, 1939)	4	10	0.7	5	1500	0.01
Hemimysis anomala (G.O. Sars, 1907)	4	1	0.5	2	1000	0.01
Limnoperna fortunei (Dunker, 1857)	10	100	0.5	5	1500	1.00E-04
Orconectes limosus (Rafinesque, 1817)	5	100	0.5	5	500	0.01
Orconectes virilis (Hagen, 1870)	4	100	0.5	5	1250	0.01
Pacifastacus leniusculus (Dana, 1852)	5	100	0.3	5	1500	0.01
Pomacea canaliculata (Lamarck, 1828)	4	10	0.5	5	500	0.01
Procambarus clarkii (Girard, 1852)	4	100	0.3	5	750	0.001
Pseudodiaptomus inopinus (Burckhardt, 1913)	4	100	0.9	5	1250	0.01
Rhithropanopeus harrisii (Gould, 1841)	5	100	0.9	5	1500	0.001
Valvata piscinalis (Muller, 1774)	5	100	0.5	5	1000	0.01

A.6 Somers' D computed from averaged AUC for each species and model

Table A 4 Somers' D computed from averaged AUC for each species and model

	CART	CTREE	KNN	LDA	LOG	NB	NNET	QDA	SVM
Corbicula fluminea (O. F. Müller, 1774)	0.96	0.94	0.97	0.84	0.88	0.78	0.97	0.90	0.98
Pseudodiaptomus inopinus (Burckhardt, 1913)	0.59	0.60	0.81	0.68	0.64	0.88	0.78	0.91	0.76
Gammarus tigrinus (Sexton, 1939)	0.90	0.91	0.96	0.90	0.92	0.83	0.96	0.92	0.96
Aedes albopictus (Skuse, 1895)	0.98	0.98	0.98	0.87	0.88	0.95	0.99	0.98	0.99
Hemimysis anomala (G.O. Sars, 1907)	0.79	0.93	0.94	0.85	0.86	0.84	0.94	0.92	0.97
Eriocheir sinensis (Milne-Edwards, 1854)	0.95	0.95	0.97	0.88	0.89	0.85	0.98	0.90	0.98
Rhithropanopeus harrisii (Gould, 1841)	0.91	0.82	0.90	0.36	0.40	0.67	0.93	0.65	0.94
Valvata piscinalis (Muller, 1774)	0.93	0.95	0.97	0.90	0.92	0.90	0.98	0.92	0.97
Cercopagis pengoi (Ostroumov, 1891)	0.80	0.69	0.87	0.67	0.67	0.81	0.89	0.79	0.89
Bithynia tentaculata (Linnaeus, 1758)	0.97	0.96	0.98	0.96	0.96	0.90	0.98	0.97	0.98
Pomacea canaliculata (Lamarck, 1828)	0.84	0.85	0.87	0.72	0.73	0.82	0.91	0.92	0.86
Limnoperna fortunei (Dunker, 1857)	0.71	0.73	0.81	0.50	0.51	0.81	0.85	0.79	0.85
Cipangopaludina japonica (von Martens, 1861)	0.77	0.82	0.90	0.61	0.62	0.82	0.92	0.80	0.94
Dikerogammarus villosus (Sowinsky, 1894)	0.85	0.83	0.91	0.87	0.89	0.82	0.96	0.93	0.97
Procambarus clarkii (Girard, 1852)	0.86	0.86	0.90	0.73	0.74	0.84	0.92	0.81	0.90
Orconectes virilis (Hagen, 1870)	0.88	0.82	0.88	0.77	0.78	0.84	0.91	0.85	0.92
Dreissena rostriformis bugensis (Andrusov, 1897)	0.85	0.73	0.84	0.64	0.64	0.69	0.89	0.72	0.91
Pacifastacus leniusculus (Dana, 1852)	0.93	0.88	0.96	0.83	0.84	0.85	0.96	0.96	0.97
Orconectes limosus (Rafinesque, 1817)	0.94	0.95	0.96	0.76	0.77	0.84	0.97	0.93	0.98
Bythotrephes longimanus (Leydig, 1860)	0.90	0.91	0.97	0.68	0.70	0.87	0.97	0.90	0.98
Dreissena polymorpha (Pallas, 1771)	0.95	0.95	0.97	0.63	0.63	0.87	0.98	0.92	0.97

A.7 List of packages used in R

Table A 5 List of packages used in R.

Description	Function	R package	Reference
OCSVM and SVM	ksvm	kernlab	(Karatzoglou et al., 2004)
RF	varSelRF	varSelRF	(Diaz-Uriarte, 2014)
LDA and QDA	lda and qda	MASS	(Venables & Ripley, 2002)
CART	rpart	rpart	(Therneau et al., 2015)
NB	NaiveBayes	klaR	(Weihs et al., 2005)
NNET	nnet	nnet	(Venables & Ripley, 2002)
LOG and kmeans	glm and kmeans	stats	(R Core Team, 2015)
KNN	knn	class	(Venables & Ripley, 2002)
CTREE	ctree	party	(Hothorn et al., 2006b)
Niche analysis		ecospat	(Broennimann et al., 2015)

A.8 Niche metrics measured across all environments

Table A 6 Niche metrics measured across all environments.

Species	Stability	D metric	Expansion	Centroid	Unfilling
Aedes albopictus (Skuse, 1895)	0.92	0.43	0.08	0.14	0.19
Bithynia tentaculata (Linnaeus, 1758)	0.53	0.03	0.47	0.34	0.95
Bythotrephes longimanus (Leydig, 1860)	0.46	0.02	0.54	0.21	0.88
Cercopagis pengoi (Ostroumov, 1891)	0.80	0.03	0.20	0.27	0.84
Cipangopaludina japonica (von Martens, 1861)	0.05	0.09	0.95	0.43	0.95
Corbicula fluminea (O. F. Müller, 1774)	0.87	0.19	0.13	0.21	0.45
Dreissena polymorpha (Pallas, 1771)	0.37	0.08	0.63	0.24	0.55
Dreissena rostriformis bugensis (Andrusov, 1897)	0.03	0.01	0.97	0.40	0.77
Eriocheir sinensis (Milne-Edwards, 1854)	0.08	0.19	0.92	0.51	0.66
Gammarus tigrinus (Sexton, 1939)	0.00	0.00	1.00	0.54	1.00
Limnoperna fortunei (Dunker, 1857)	0.57	0.09	0.43	0.28	0.69
Orconectes limosus (Rafinesque, 1817)	0.06	0.13	0.94	0.38	0.63
Orconectes virilis (Hagen, 1870)	0.60	0.14	0.40	0.20	0.09
Pacifastacus leniusculus (Dana, 1852)	0.38	0.11	0.62	0.44	0.82
Pomacea canaliculata (Lamarck, 1828)	0.66	0.25	0.34	0.27	0.23
Potamopyrgus antipodarum (Gray, 1843)	0.07	0.20	0.93	0.44	0.29
Procambarus clarkii (Girard, 1852)	0.98	0.21	0.02	0.15	0.51
Pseudodiaptomus inopinus (Burckhardt, 1913)	0.00	0.00	1.00	0.89	1.00
Rhithropanopeus harrisii (Gould, 1841)	0.31	0.18	0.69	0.48	0.18
Valvata piscinalis (Muller, 1774)	0.52	0.06	0.48	0.36	0.84

A.9 Niche metrics measured in analogous environments

Table A 7 Niche metrics measured in analogous environments.

Species name	Stability	D metric	Expansion	Centroid	Unfilling
Aedes albopictus (Skuse, 1895)	0.92	0.43	0.08	0.16	0.19
Bithynia tentaculata (Linnaeus, 1758)	0.56	0.03	0.44	0.39	0.94
Bythotrephes longimanus (Leydig, 1860)	0.47	0.02	0.53	0.43	0.77
Cercopagis pengoi (Ostroumov, 1891)	0.80	0.03	0.20	0.31	0.63
Cipangopaludina japonica (von Martens, 1861)	0.16	0.09	0.84	0.60	0.84
Corbicula fluminea (O. F. Müller, 1774)	0.89	0.19	0.11	0.12	0.39
Dreissena polymorpha (Pallas, 1771)	0.49	0.08	0.51	0.30	0.53
Dreissena rostriformis bugensis (Andrusov, 1897)	0.07	0.01	0.93	0.59	0.74
Eriocheir sinensis (Milne-Edwards, 1854)	0.62	0.19	0.38	0.11	0.39
Limnoperna fortunei (Dunker, 1857)	0.66	0.09	0.34	0.42	0.54
Orconectes limosus (Rafinesque, 1817)	0.08	0.13	0.92	0.54	0.62
Orconectes virilis (Hagen, 1870)	0.64	0.14	0.36	0.21	0.08
Pacifastacus leniusculus (Dana, 1852)	0.38	0.11	0.62	0.43	0.67
Pomacea canaliculata (Lamarck, 1828)	0.67	0.25	0.33	0.30	0.23
Potamopyrgus antipodarum (Gray, 1843)	0.15	0.20	0.85	0.52	0.26
Procambarus clarkii (Girard, 1852)	0.98	0.21	0.02	0.23	0.51
Rhithropanopeus harrisii (Gould, 1841)	0.35	0.18	0.65	0.66	0.09
Valvata piscinalis (Muller, 1774)	0.54	0.06	0.46	0.39	0.38

A.10 Kendall correlation test results between AUC and niche metrics

Table A 8 Kendall correlation test results between AUC and niche metrics.

Niche index	tau	p value
Stability	0.16	0.50
D metric	0.13	0.59
Unfilling	0.09	0.70
Centroid	-0.27	0.25

Appendix B **Supplement to chapter 4**

B.1 Inflated response curves for the nine models of each species along the environmental variables that contribute the most to extrapolation in New Zealand. The black line indicates the response curve of the variable after accounting the average effects of the other variables used to fit the model. The blue lines indicate combinations of environmental predictors that are in the calibration data whereas dotted grey lines indicate extrapolation to novel combinations. The plots represent 150 Latin hypercube samples from all possible combinations of environmental variables used in the model fitting process (minimum, maximum, median, mean and quartile). LOG: logistic regression, NNET: artificial neural network, CART: classification and regression trees, QDA: quadratic discriminant analysis, LDA: linear discriminant analysis, NB: naïve Bayes, CTREE: conditional trees, KNN: k-nearest neighbours, SVM: support vector machines.

Figure B 1 *Bithynia tentaculata:* cbio06 (Min temperature of coldest month).

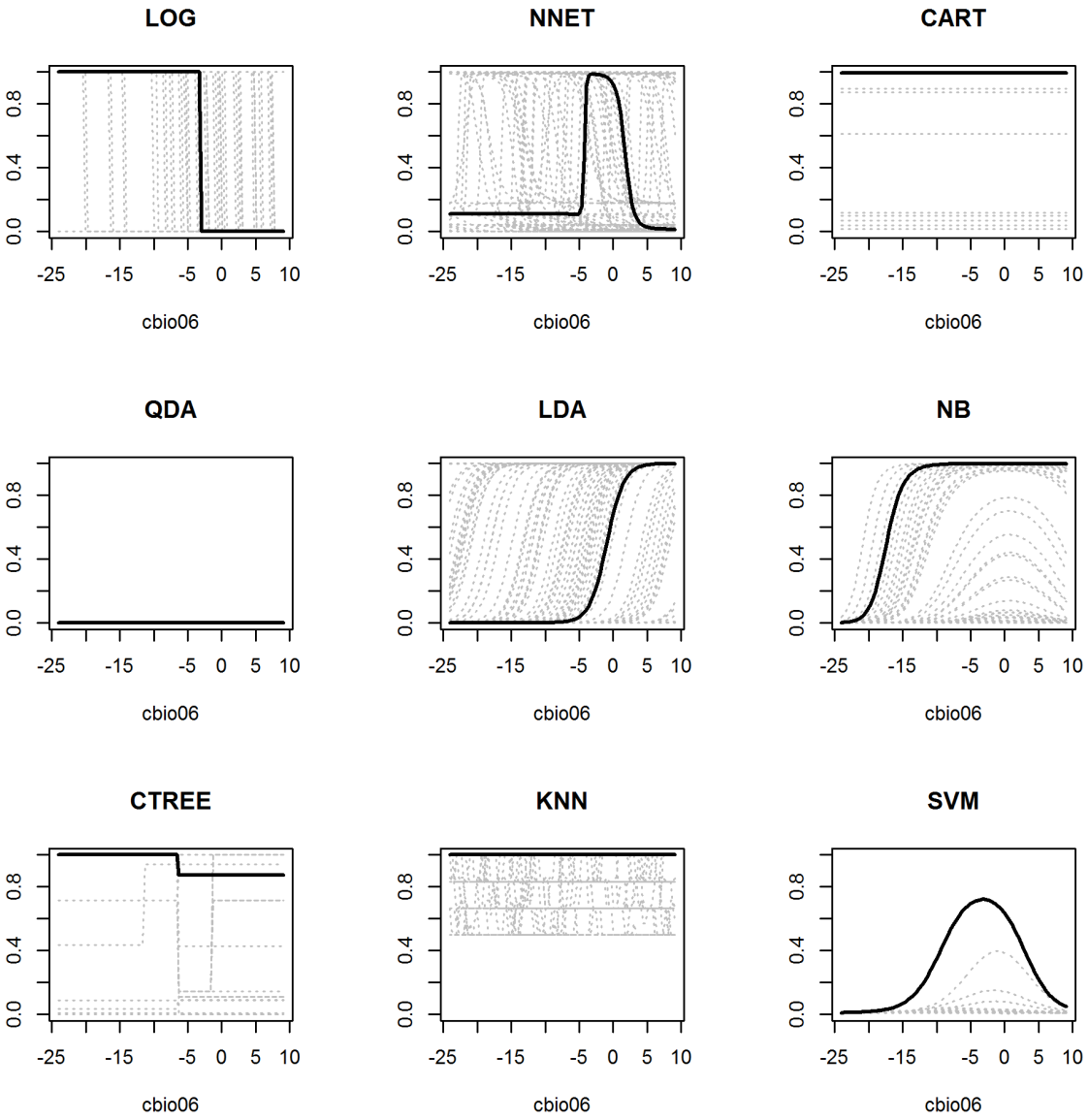


Figure B 2 *Bithynia tentaculata:* cbio10 (Mean temperature of warmest quarter).

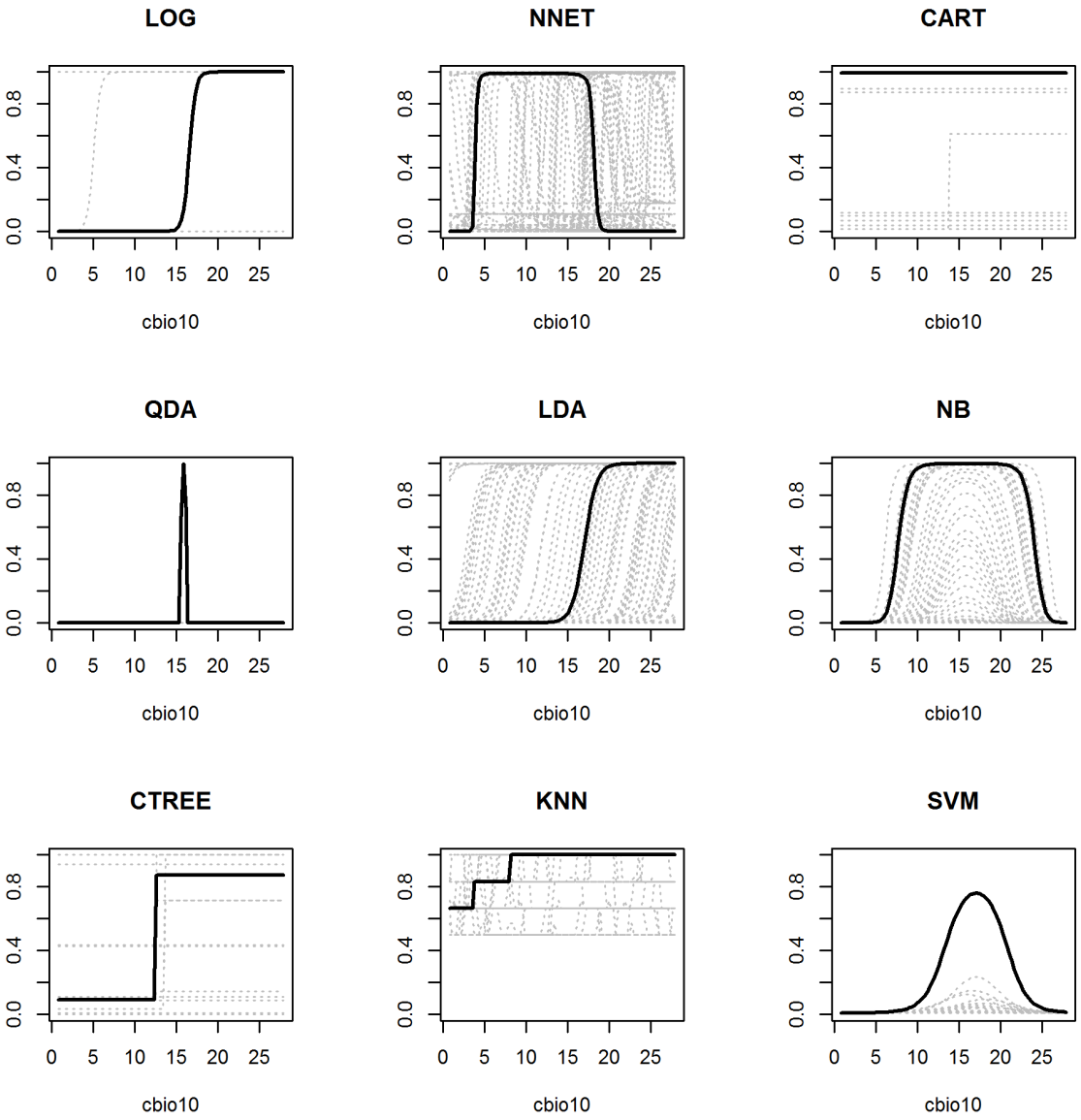


Figure B 3 *Bythotrephes longimanus:* cbio06 (Min temperature of coldest month).

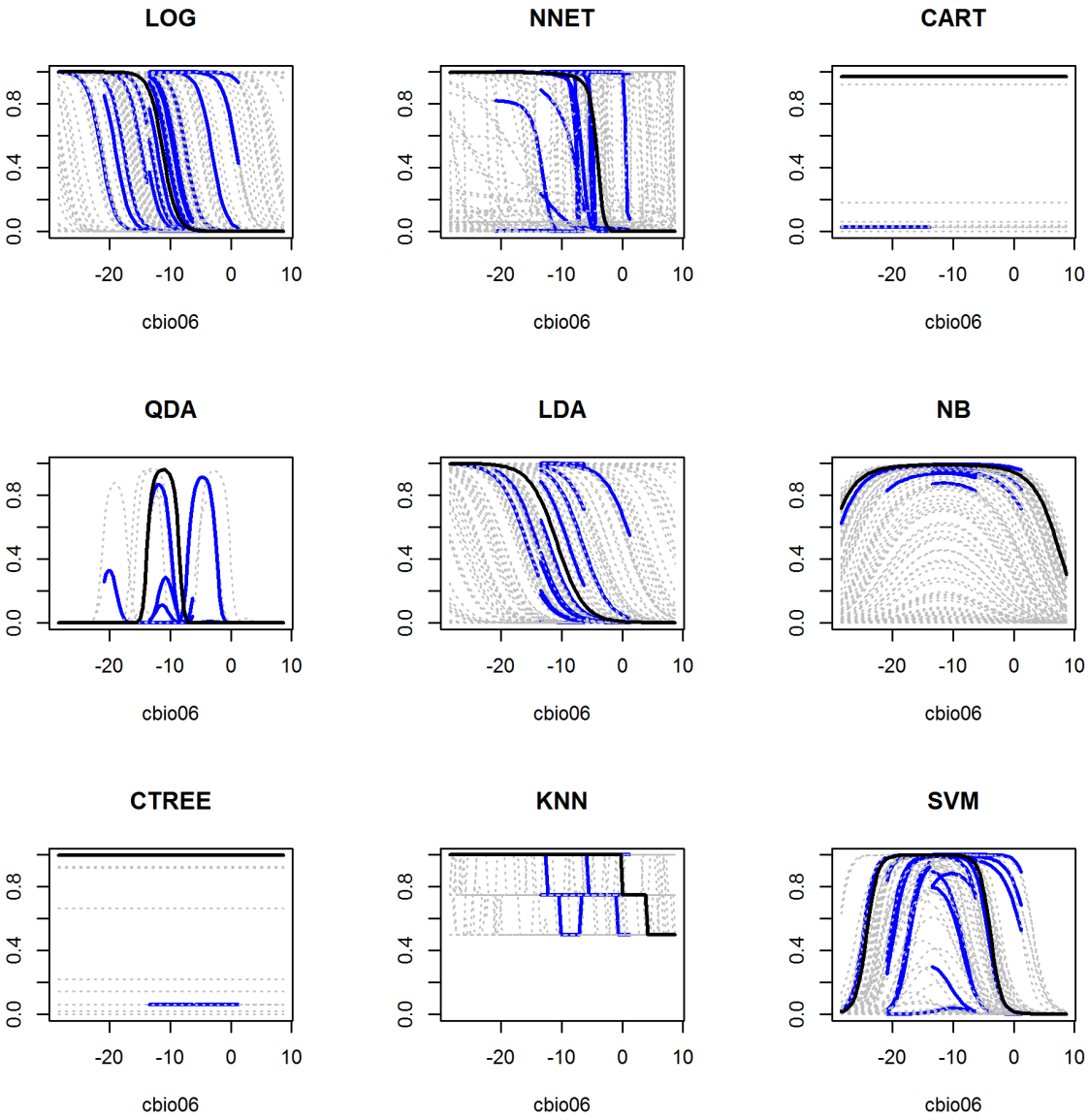


Figure B 4 *Bythotrephes longimanus:* cbio18 (Precipitation of warmest quarter).

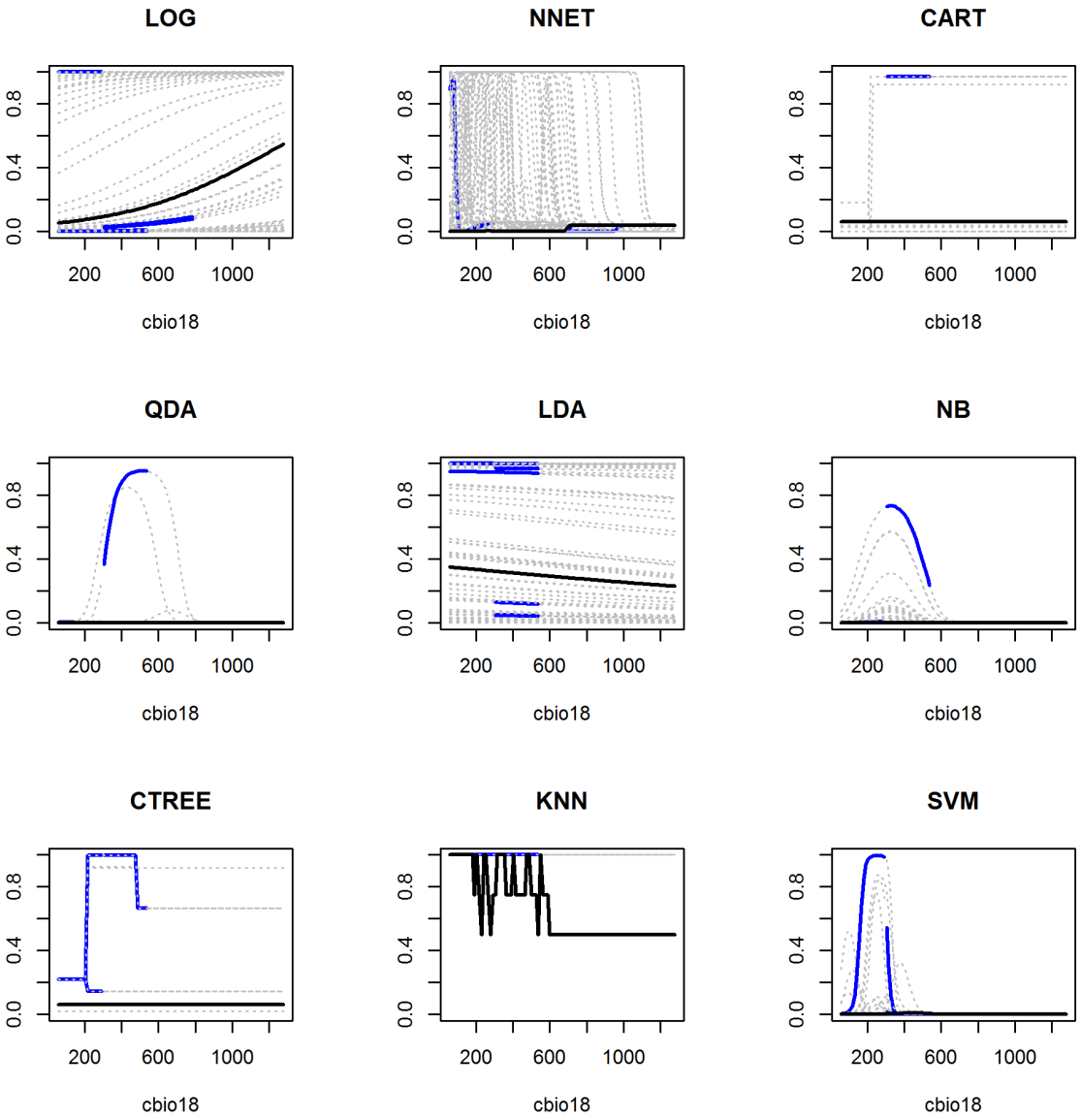


Figure B 5 *Cercopagis pengoi*: cbio03 (Isothermality = [temperature annual range/temperature annual range]*100).

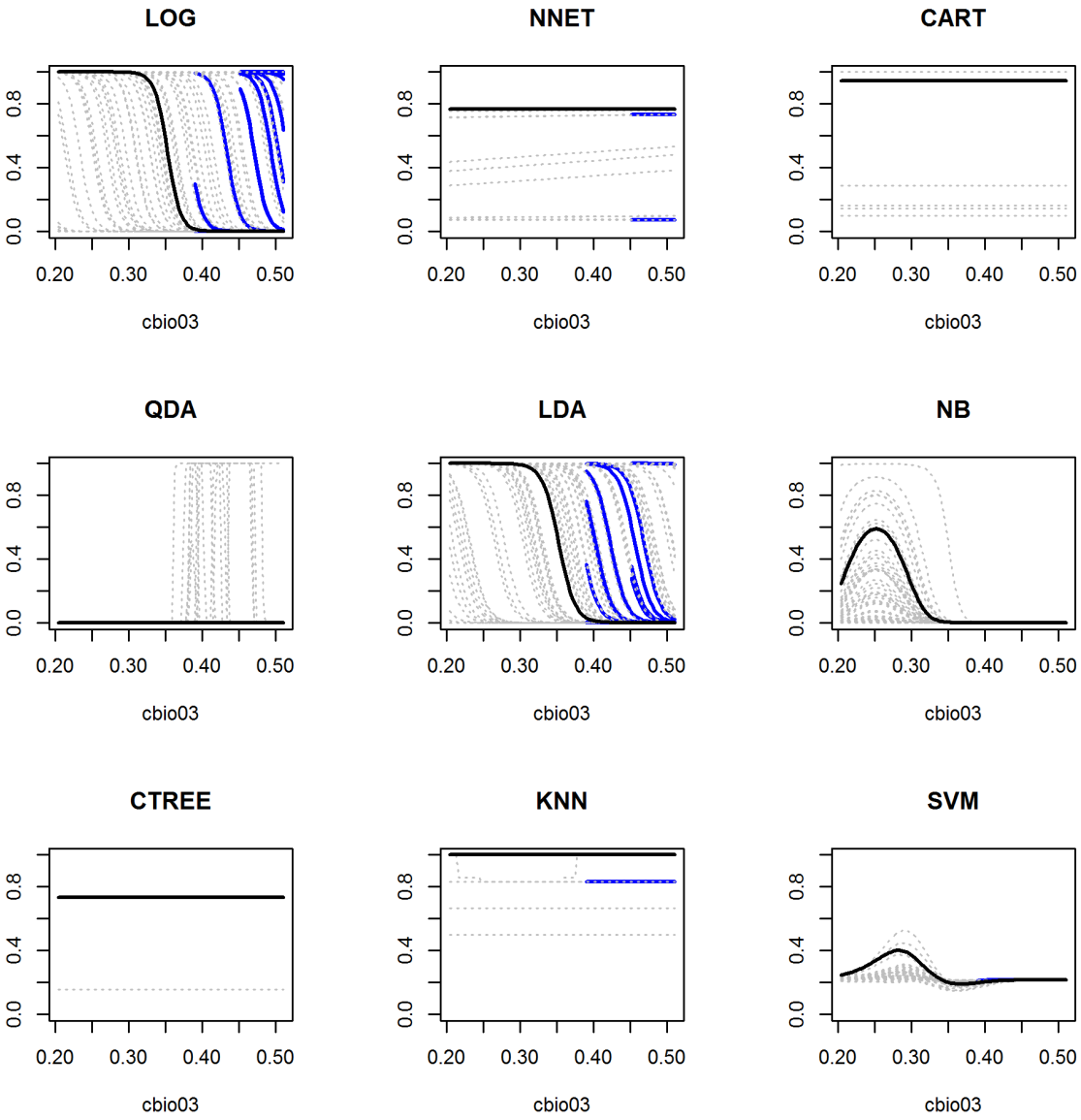


Figure B 6 *Cipangopaludina japonica:* cbio10 (Mean temperature of the warmest quarter).

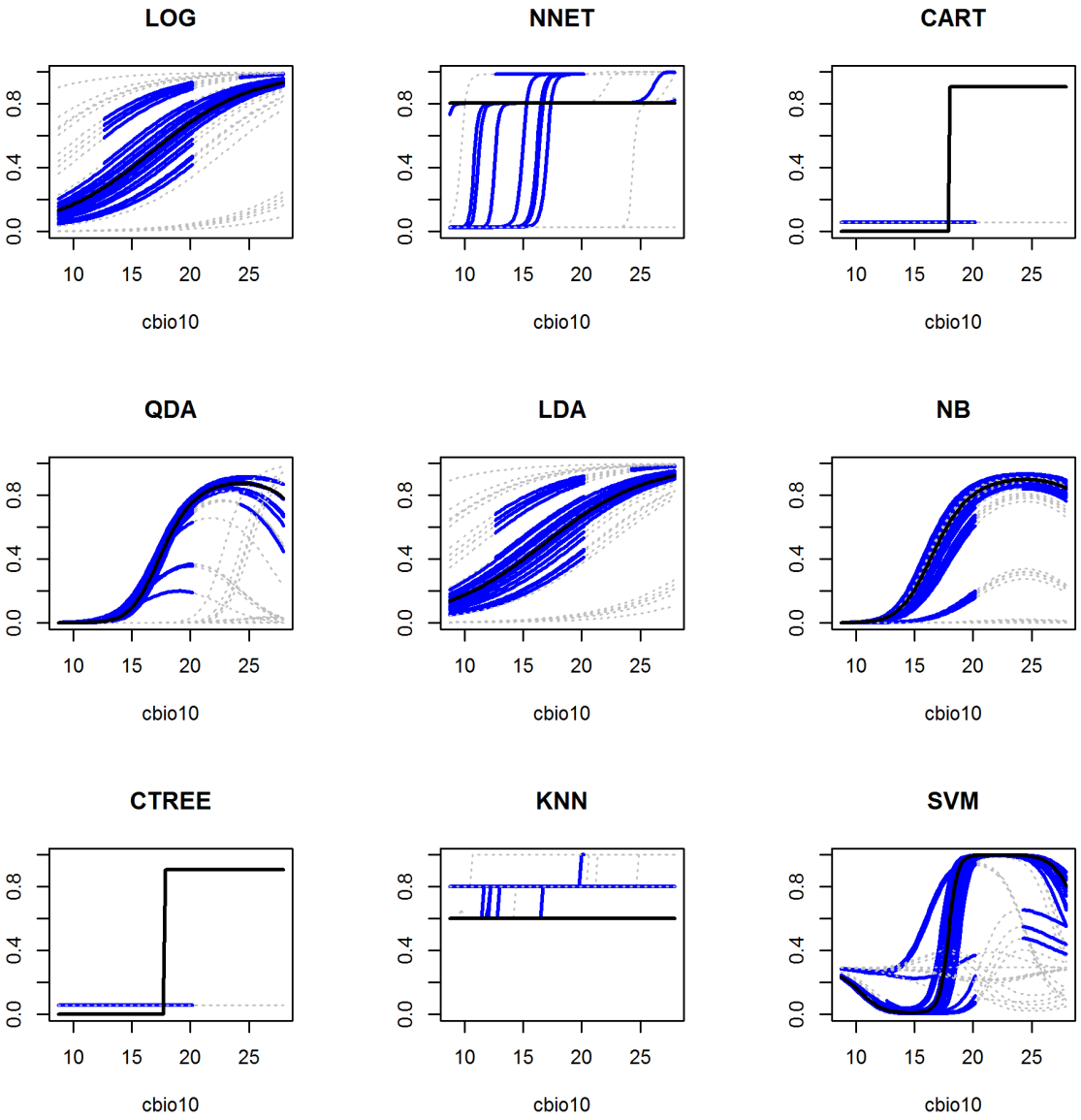


Figure B 7 *Cipangopaludina japonica:* cbio18 (Precipitation of warmest quarter).

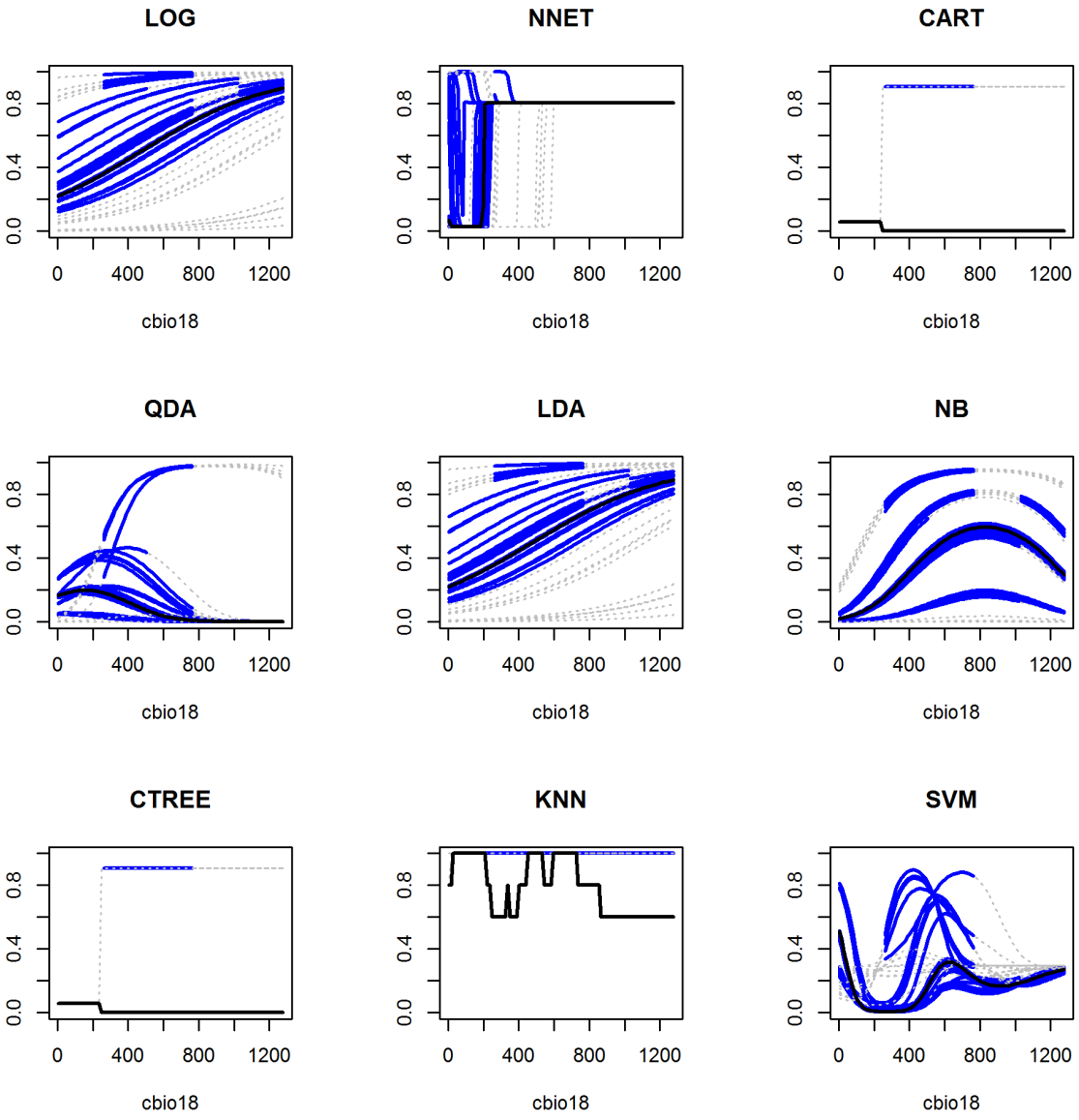


Figure B 8 *Corbicula fluminea:* cbio14 (Precipitation of driest month).

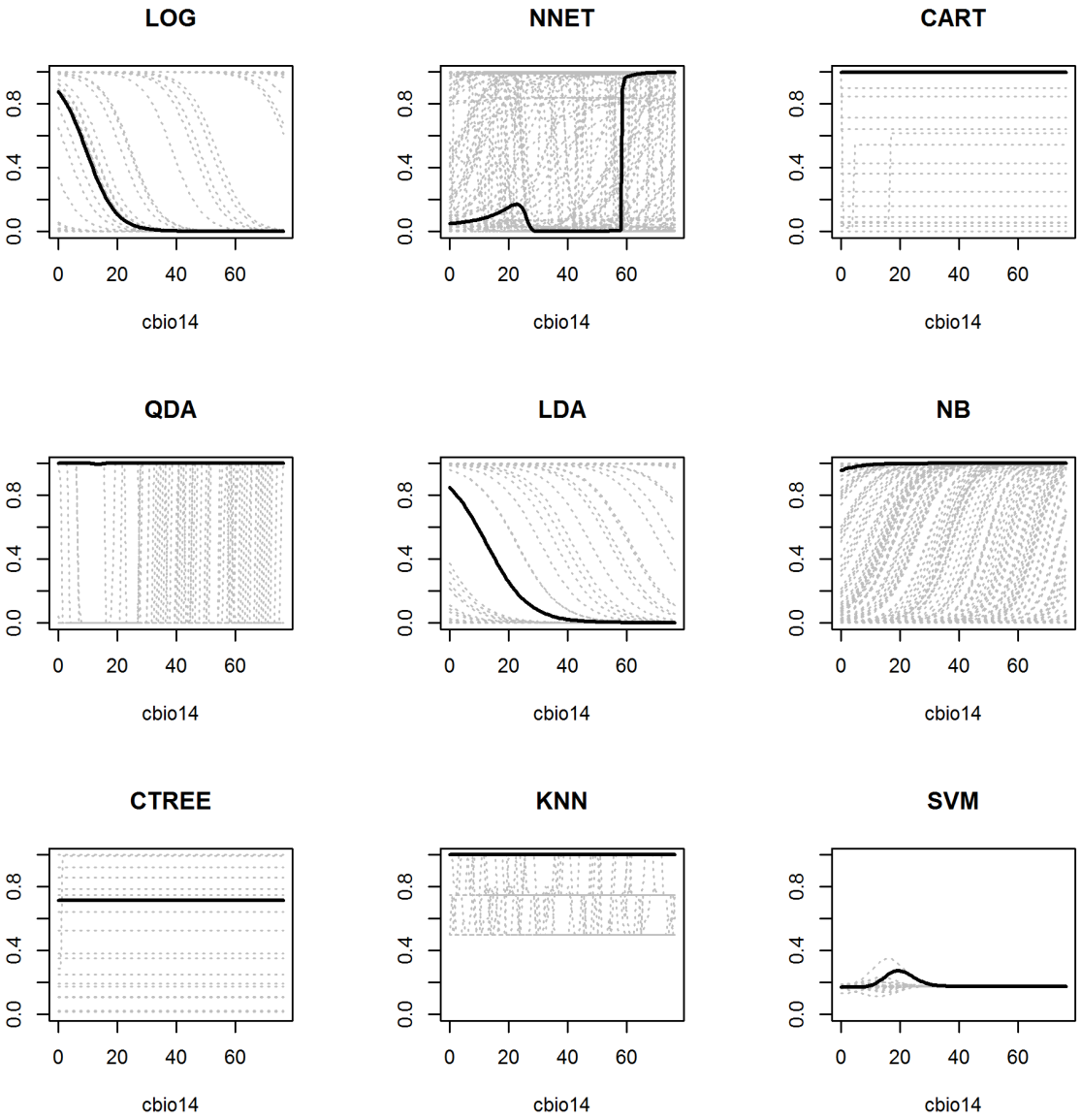


Figure B 9 *Corbicula fluminea:* cbio17 (Precipitation of the driest quarter).

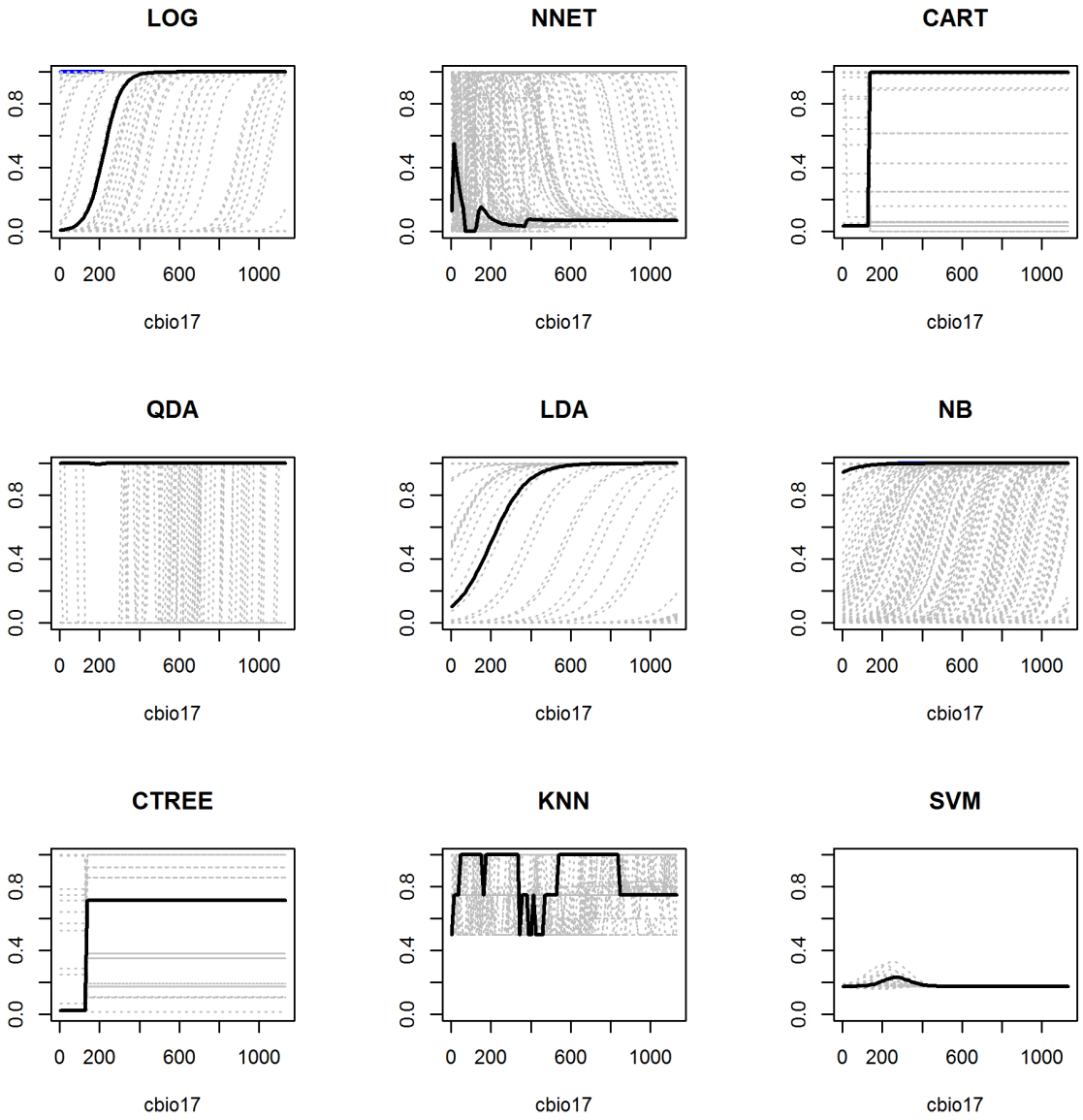


Figure B 10 *Dikerogammarus villosus:* cbio04 (Temperature seasonality).

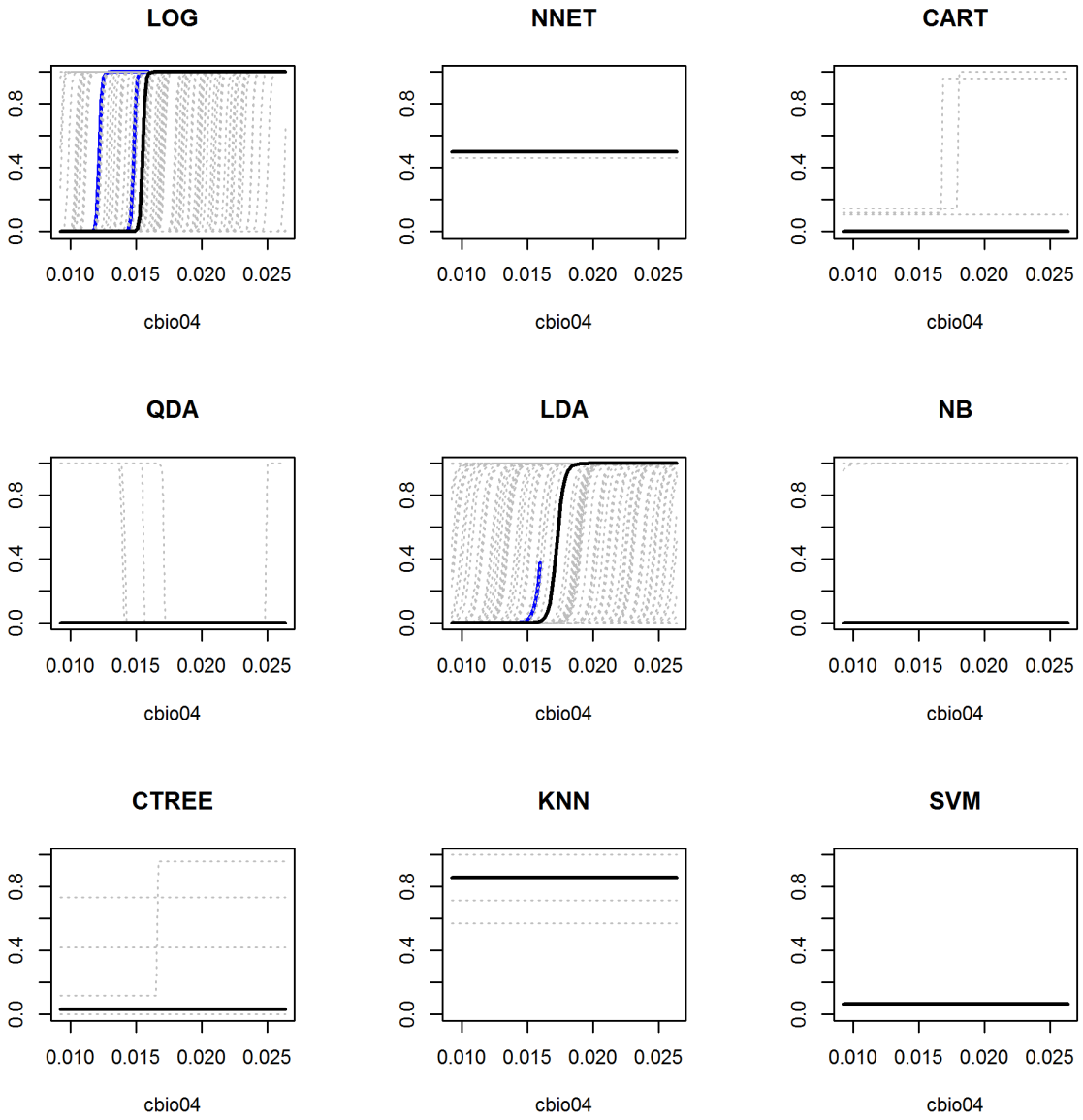


Figure B 11 *Dikerogammarus villosus:* cbio12 (Annual precipitation).

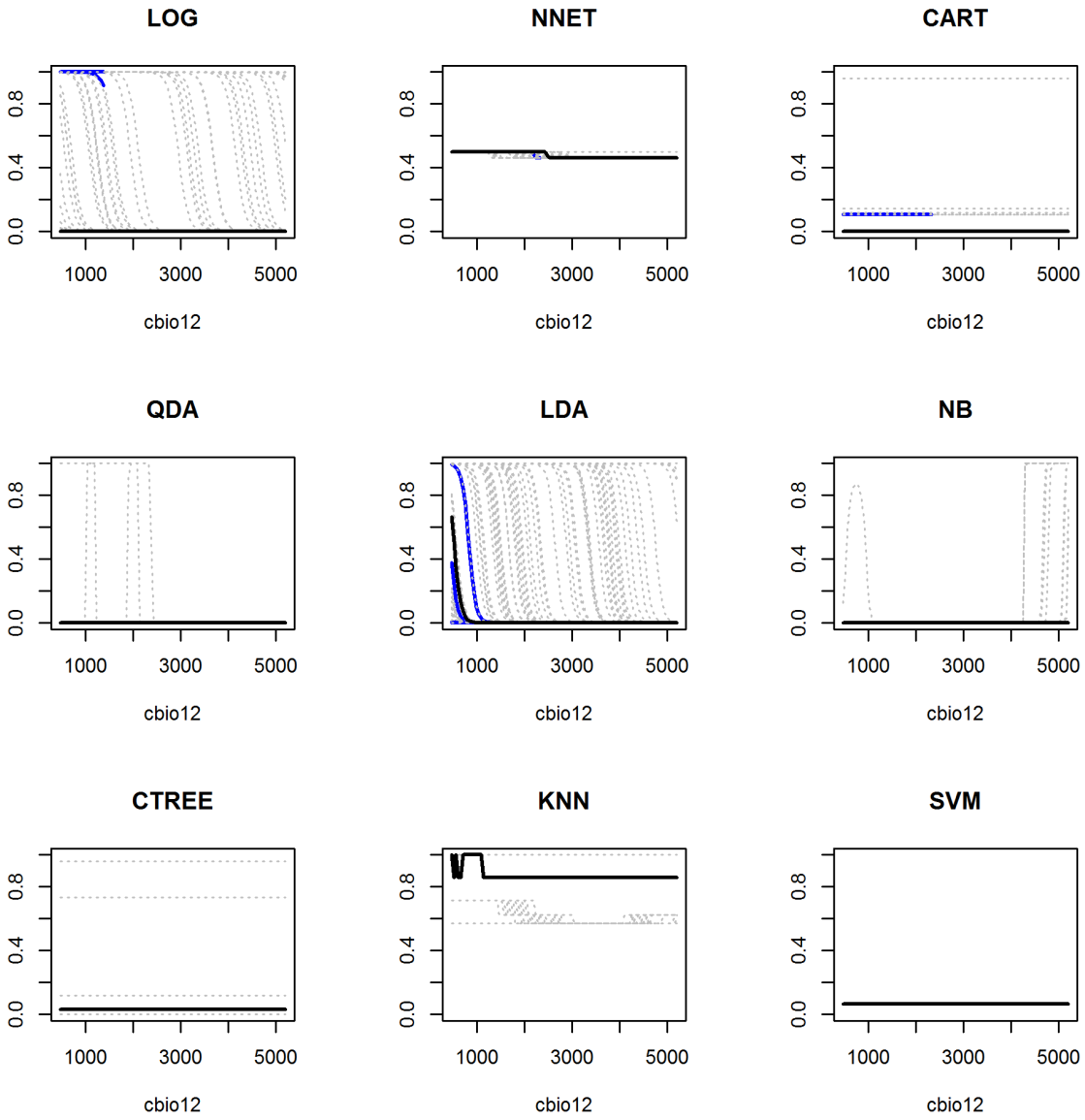


Figure B 12 *Dikerogammarus villosus :* cbio20 (Annual mean radiation).

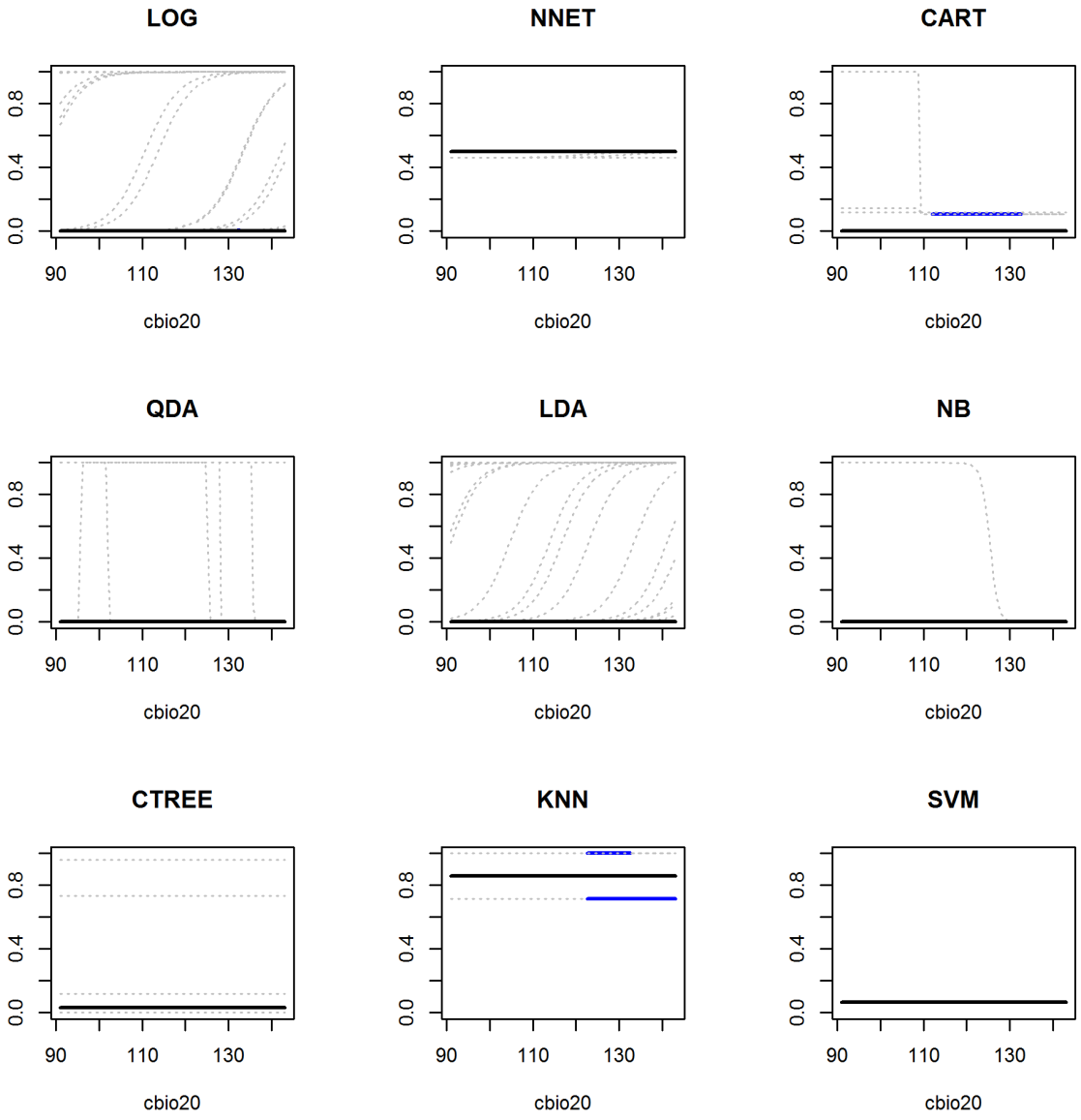


Figure B 13 *Dikerogammarus villosus :* cbio22 (Lowest weekly radiation).

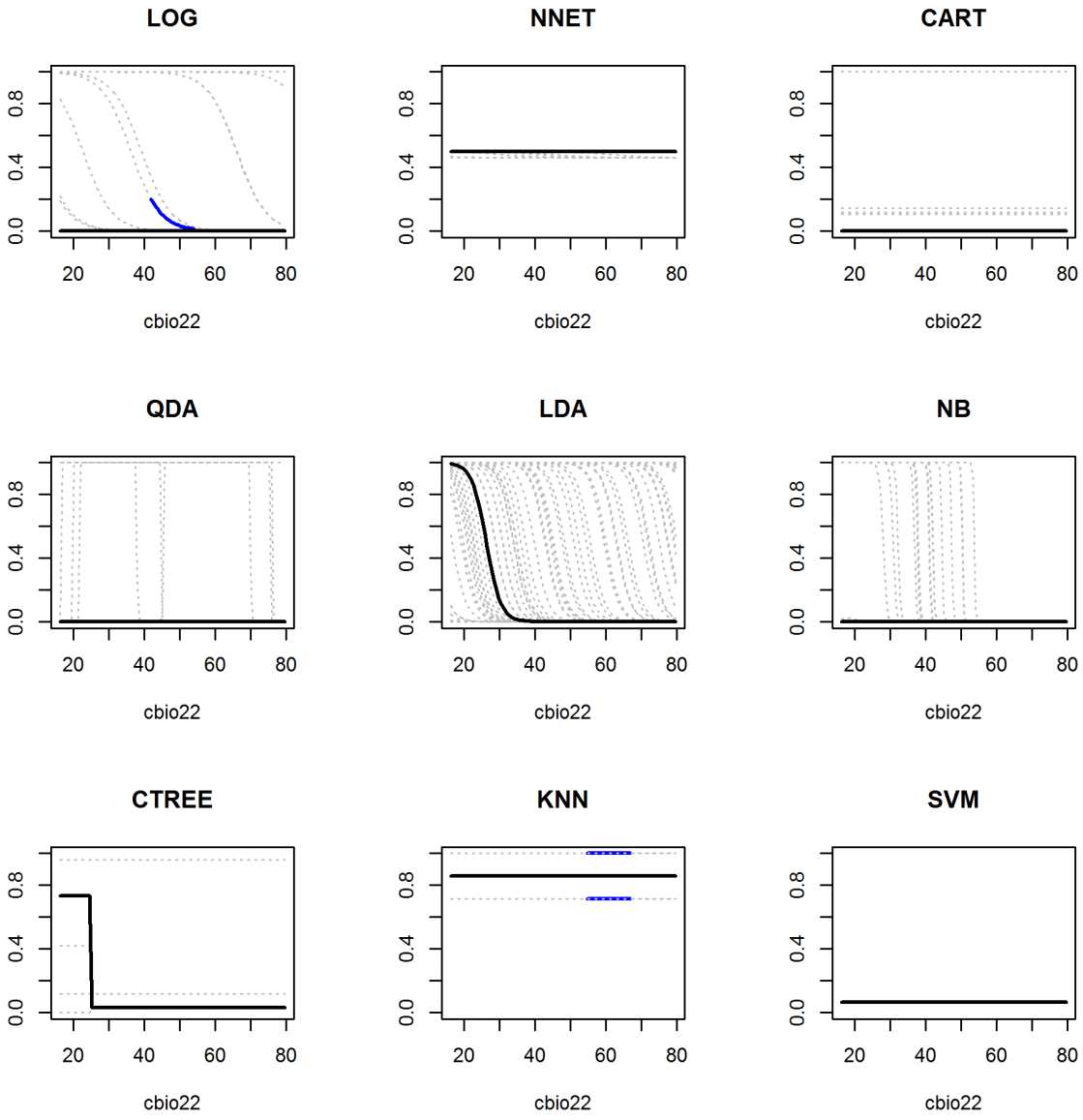


Figure B 14 *Dreissena polymorpha:* cbio12 (Annual precipitation).

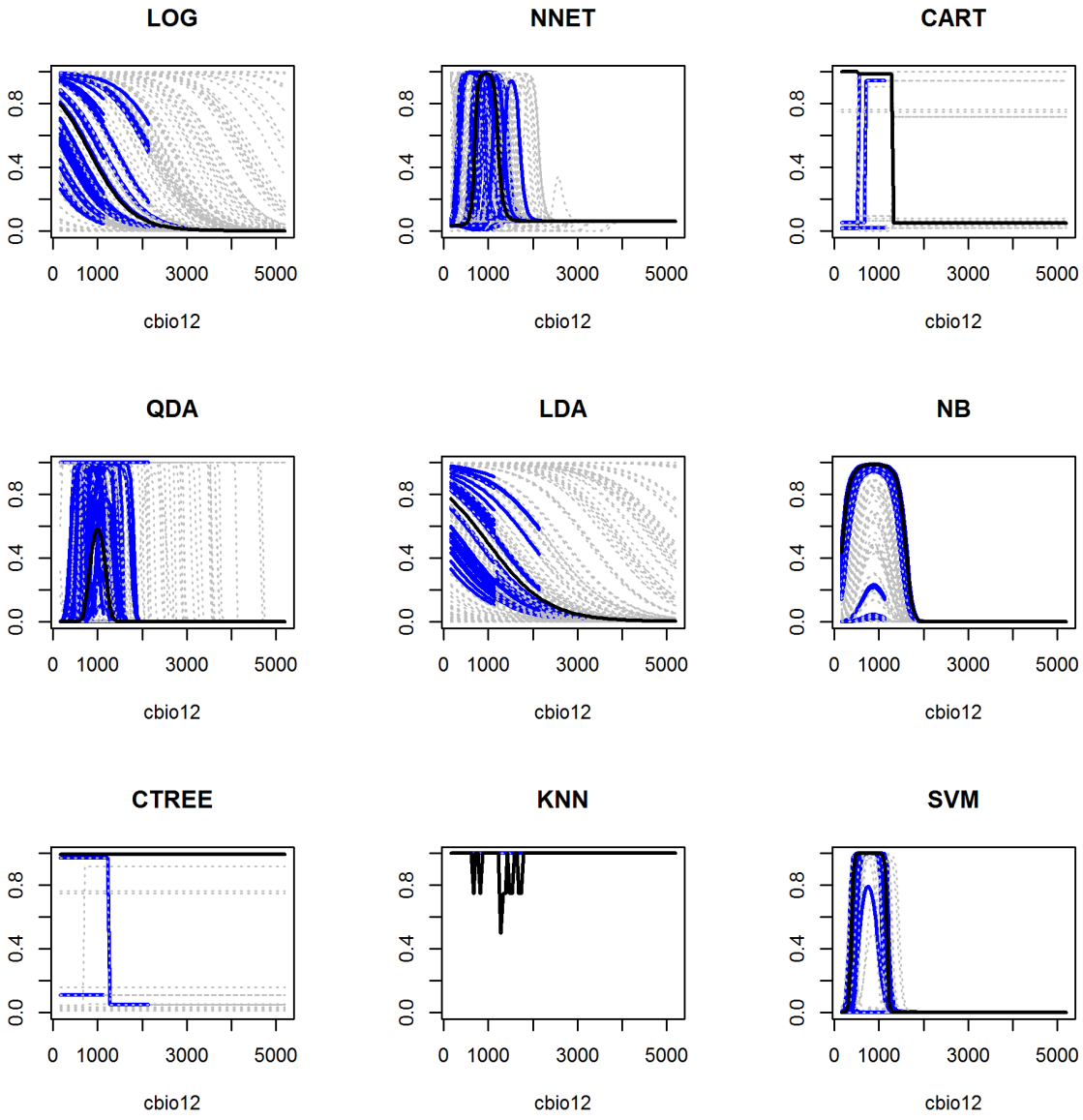


Figure B 15 *Dreissena bugensis:* cbio03 (Isothermality=[temperature annual range/temperature annual range]*100).

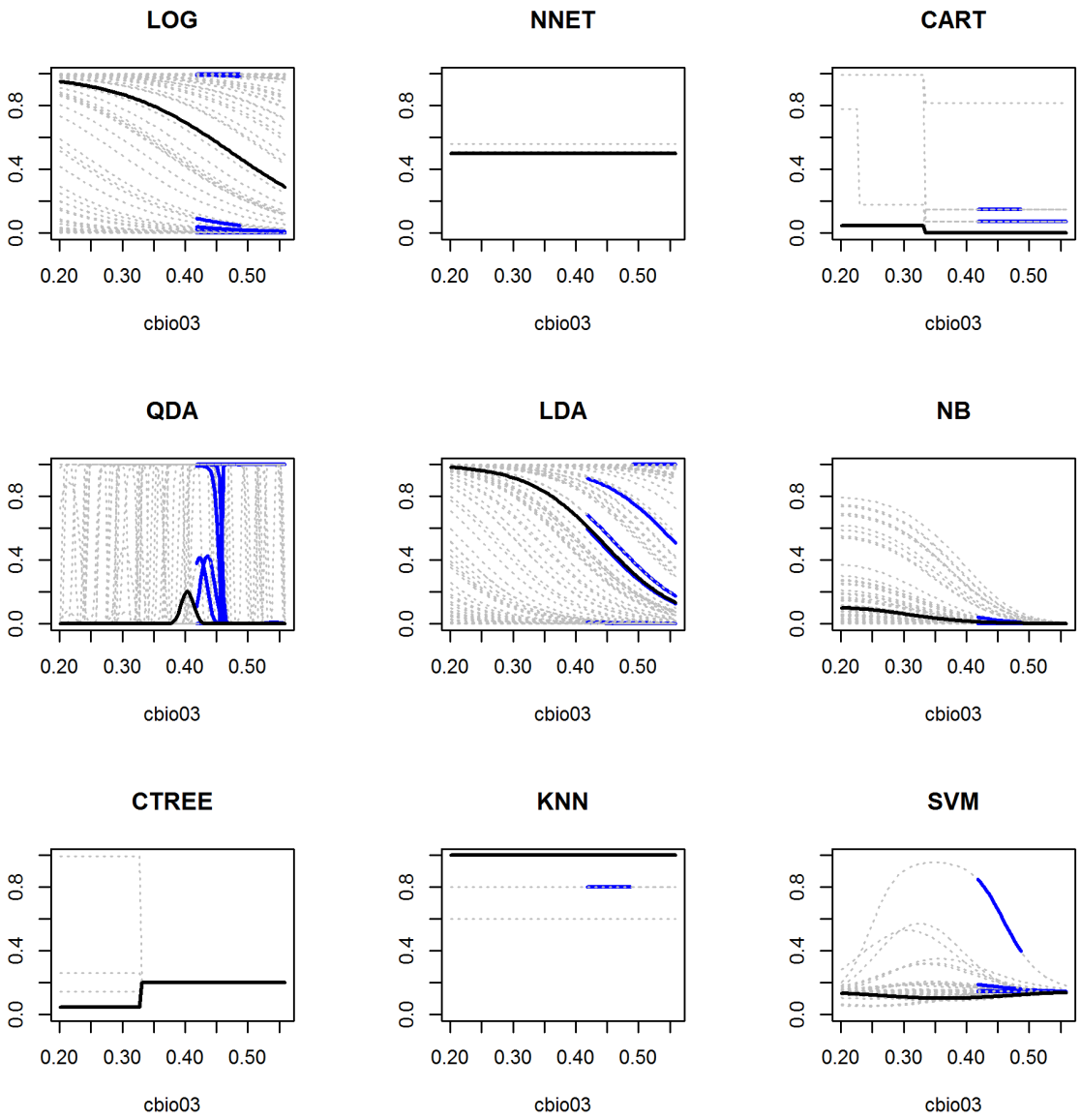


Figure B 16 *Dreissena bugensis:* cbio04 (Temperature seasonality).

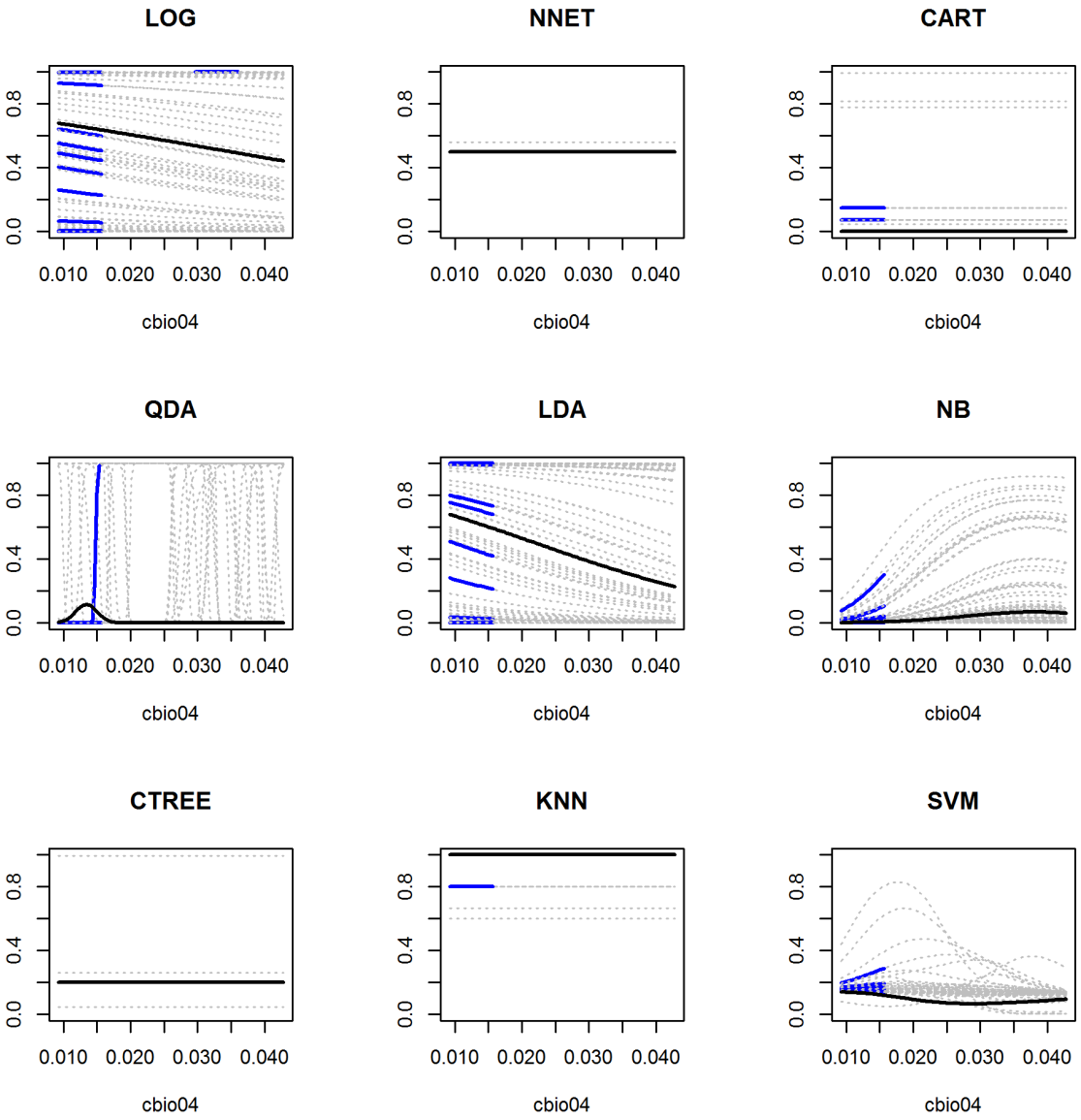


Figure B 17 *Dreissena bugensis:* cbio14 (Precipitation of driest month).

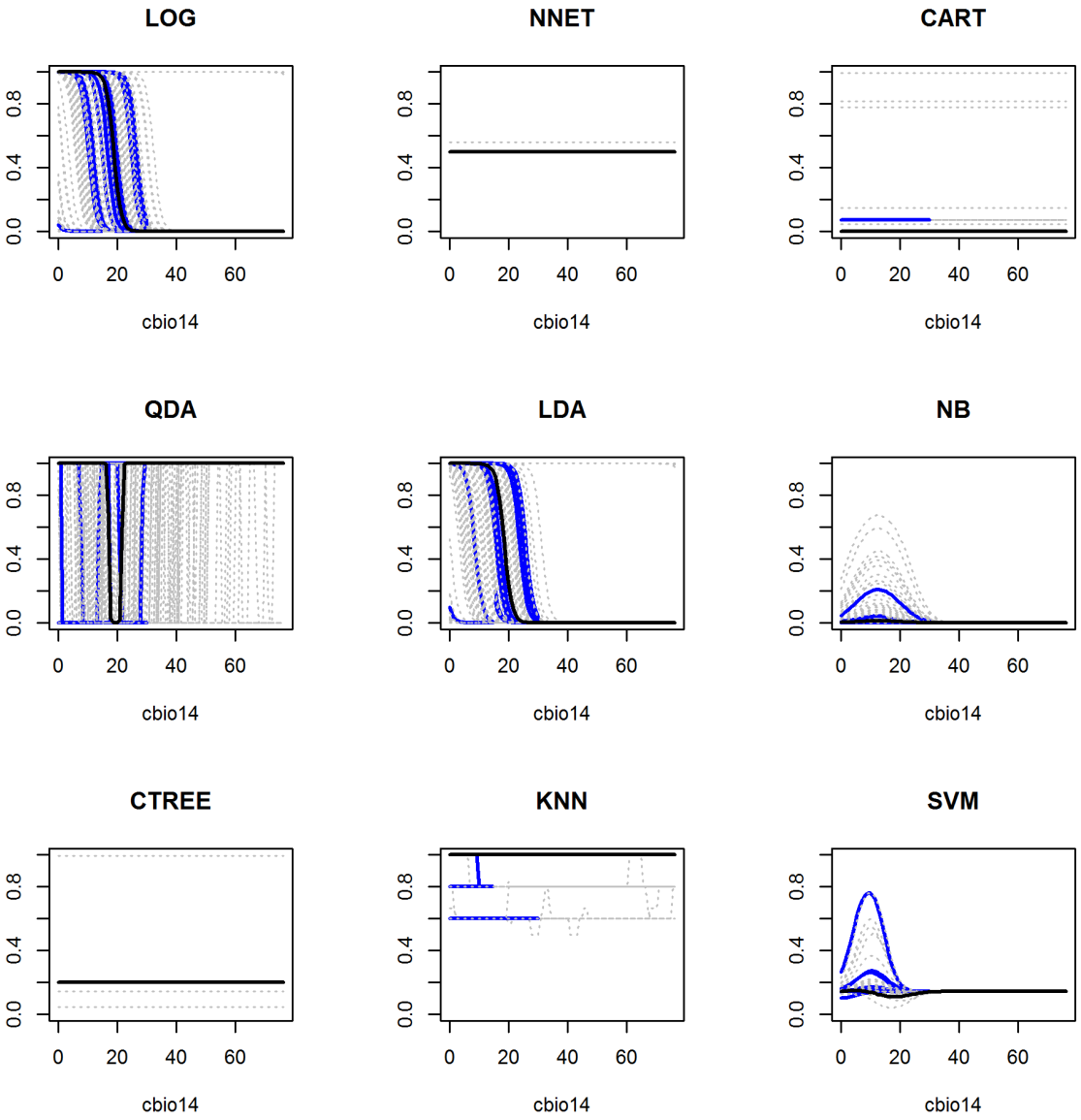


Figure B 18 *Dreissena bugensis:* cbio17 (Precipitation of driest quarter).

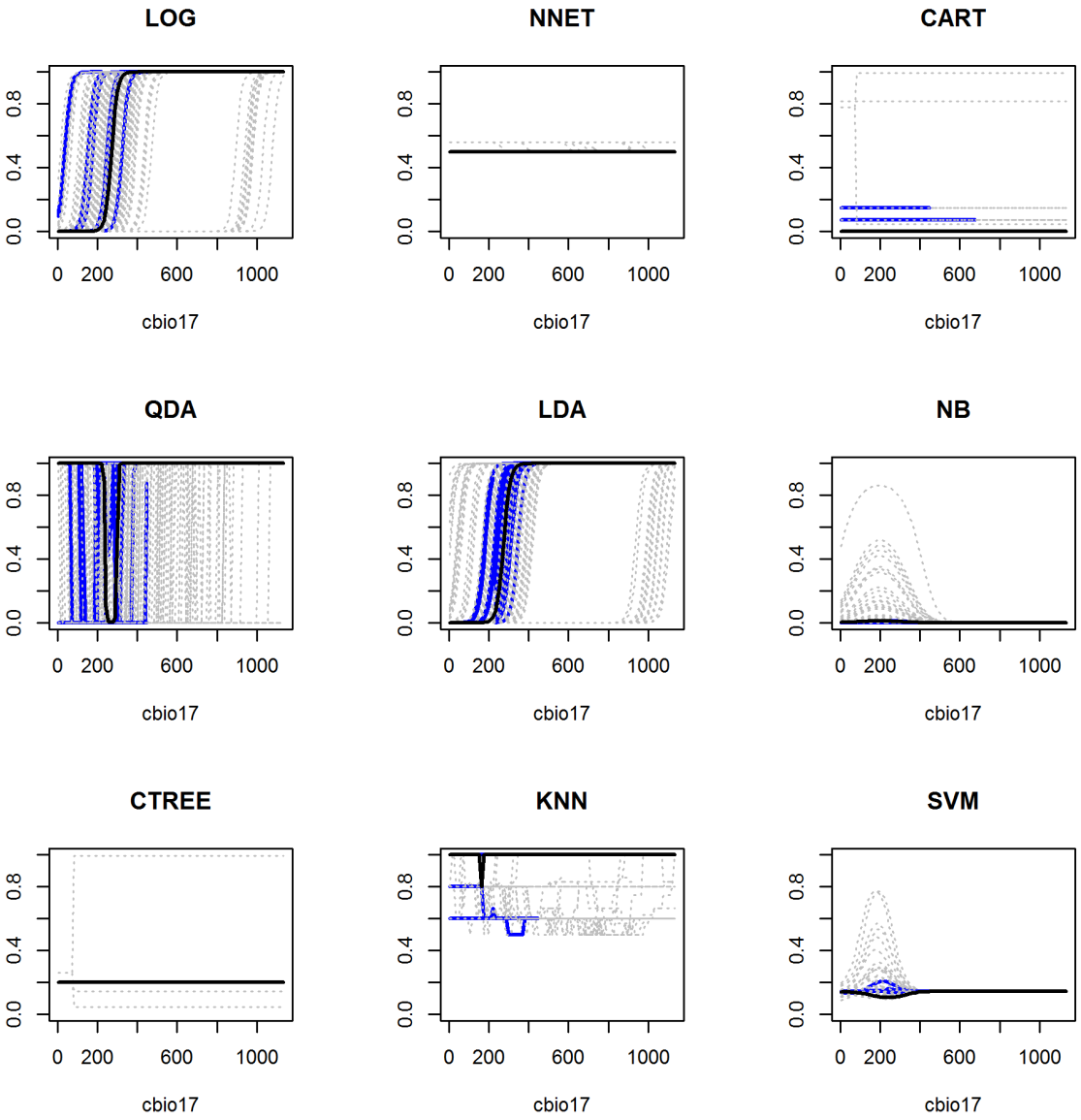


Figure B 19 *Dreissena bugensis:* cbio19 (Precipitation of coldest quarter).

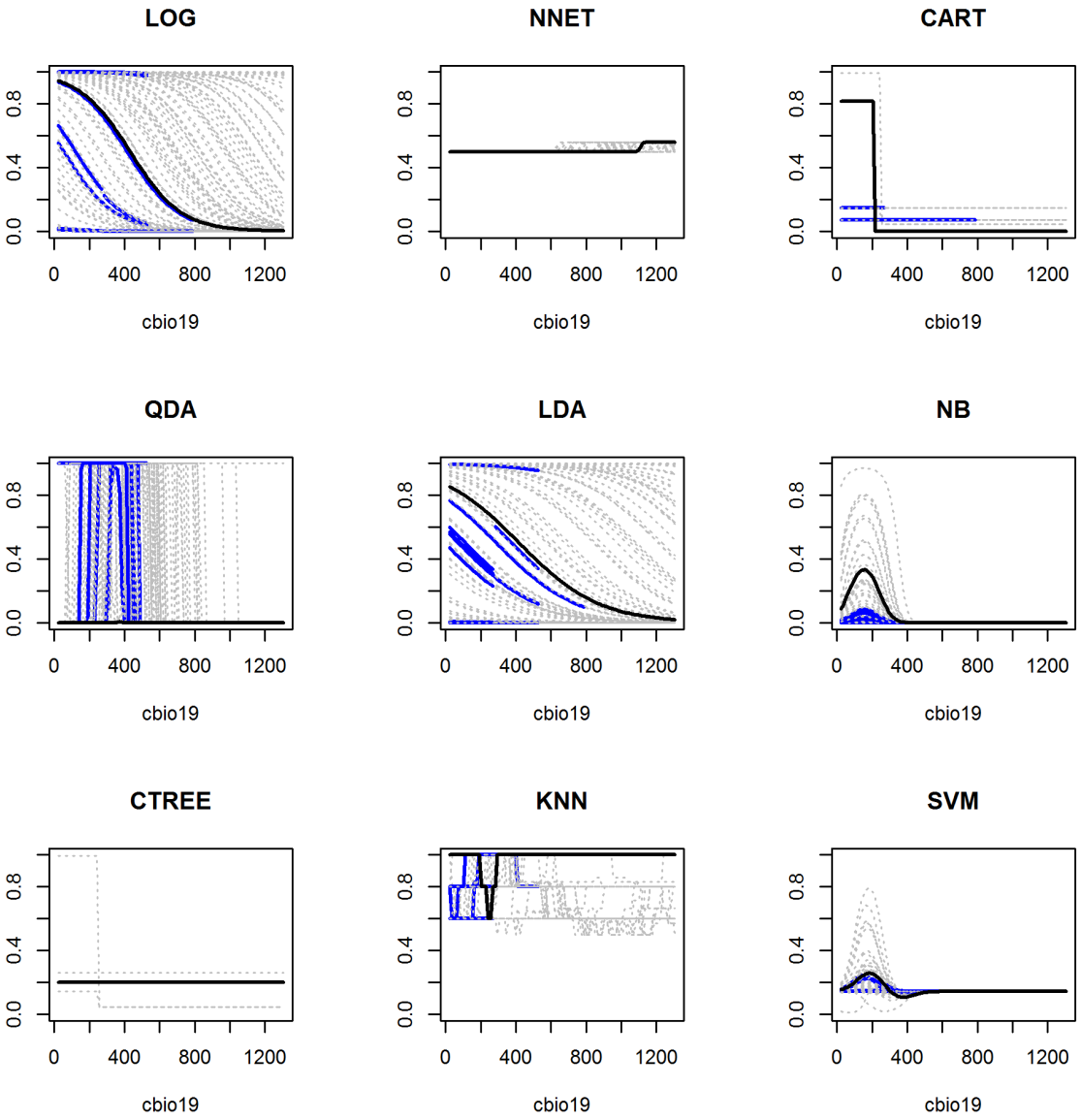


Figure B 20 *Eriocheir sinensis*: cbio01 (Annual mean temperature).

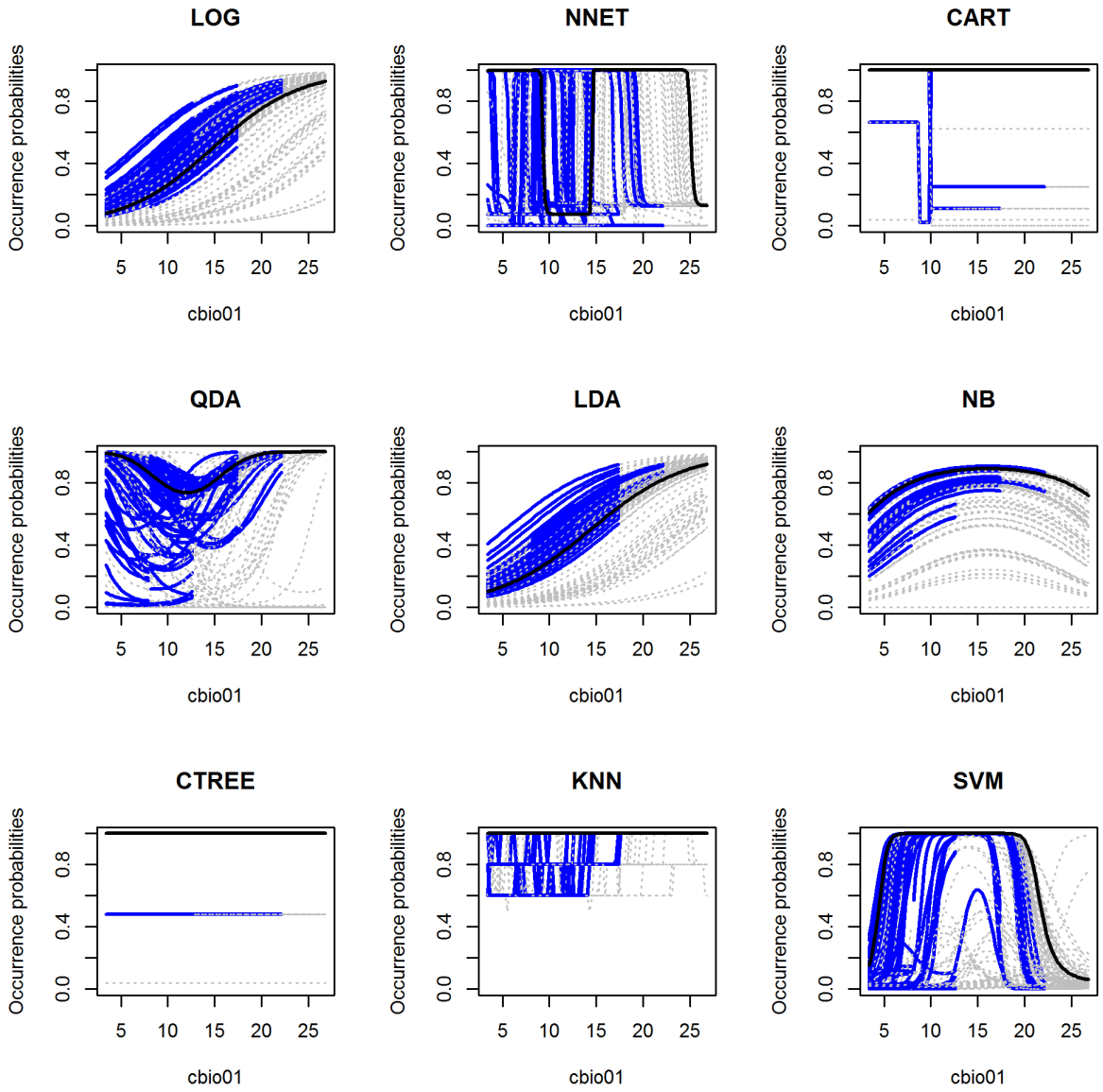


Figure B 21 *Eriocheir sinensis*: cbio03 (Isothermality=[temperature annual range/temperature annual range]*100).

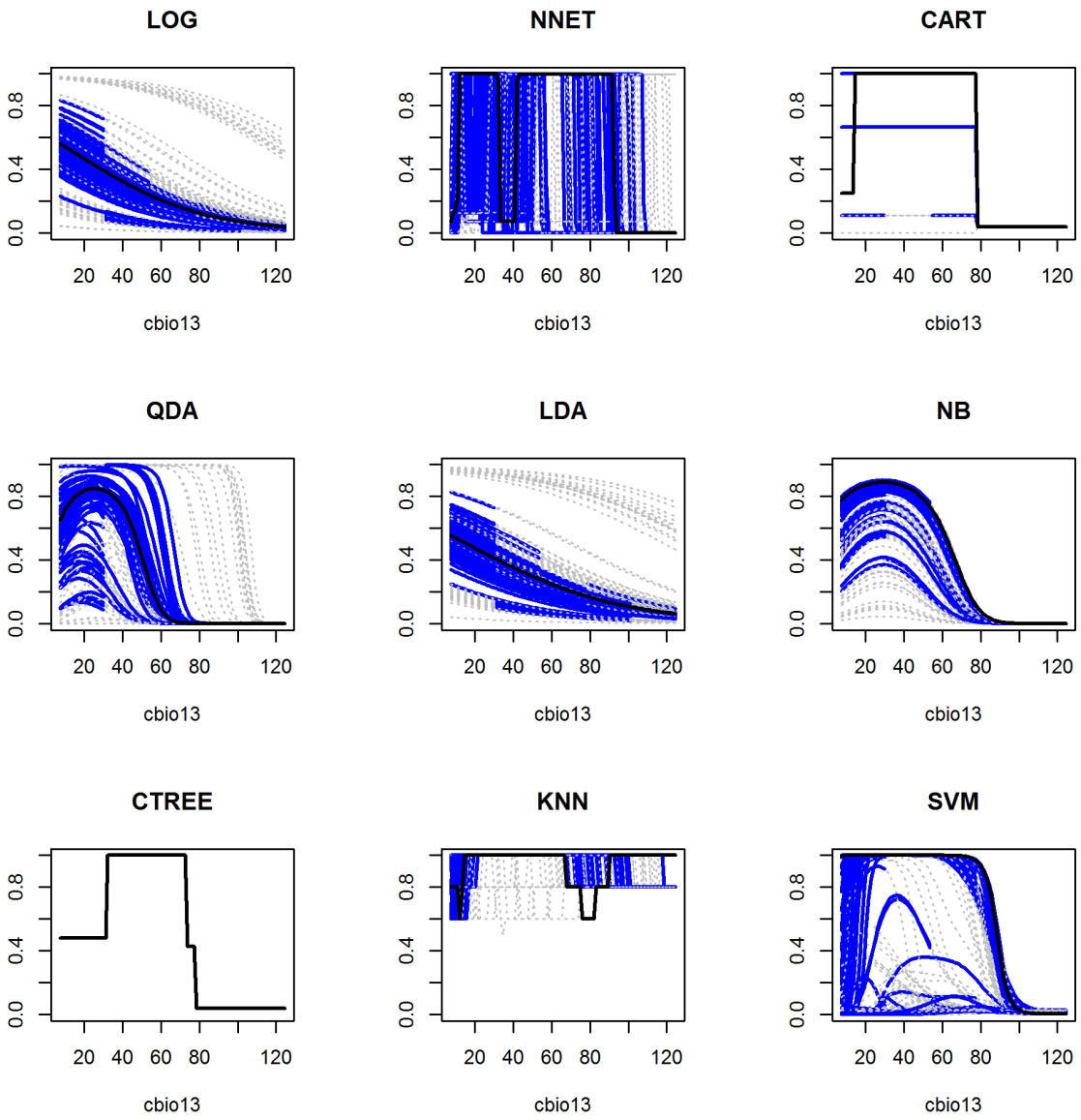


Figure B 22 *Gammarus tigrinus:* cbio01 (Annual mean temperature).

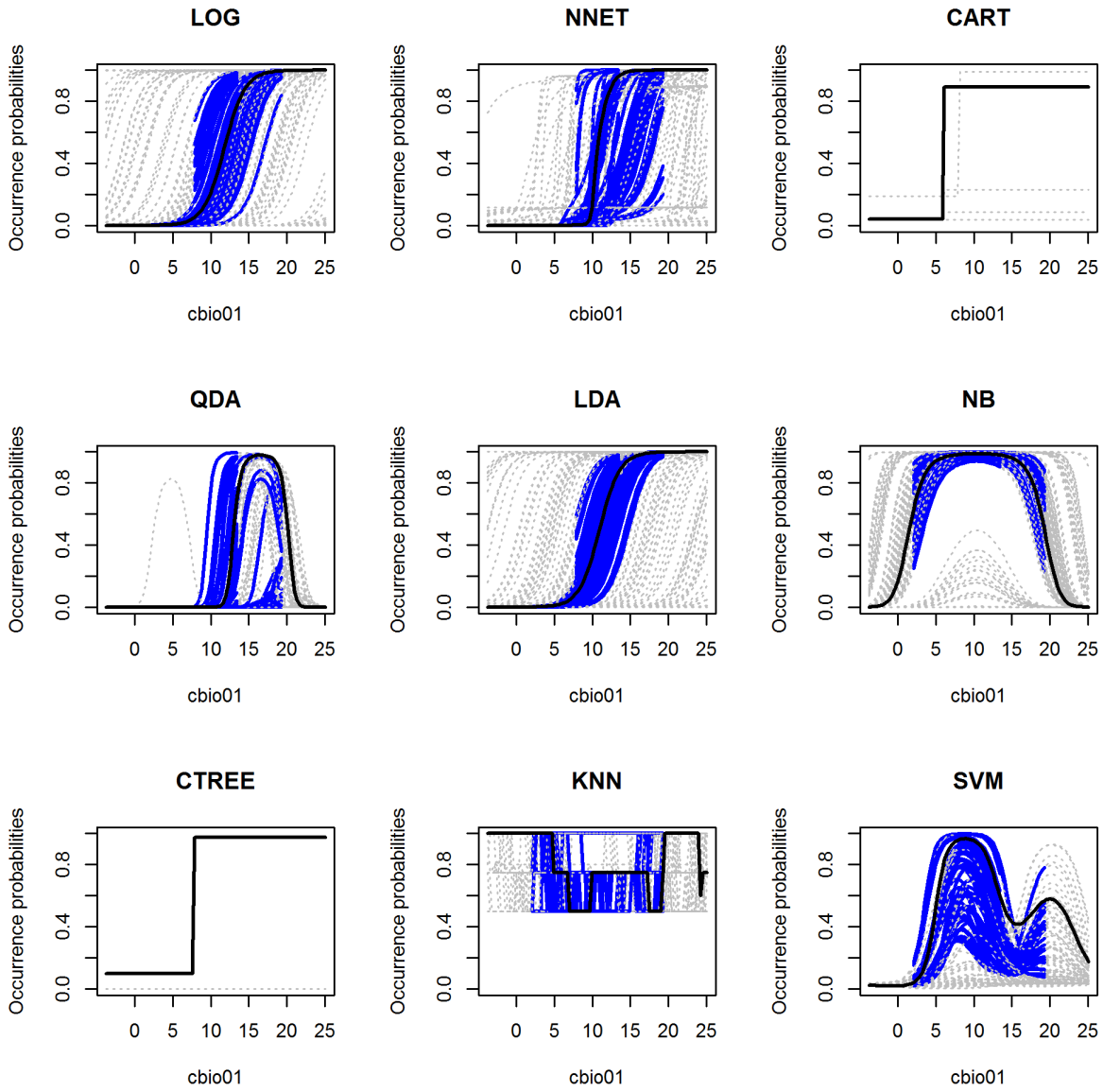


Figure B 23 *Gammarus tigrinus:* cbio07 (Temperature annual range).

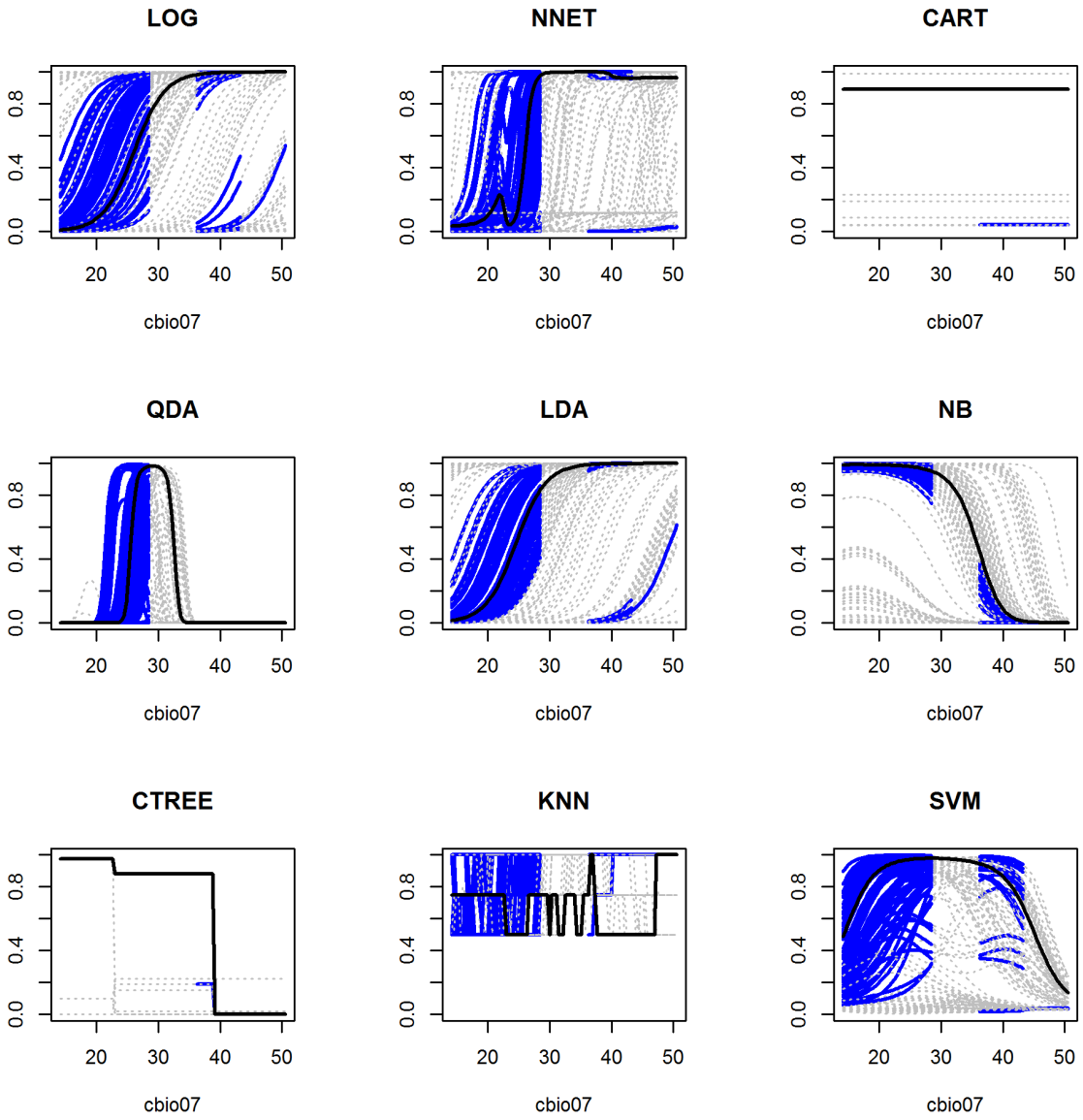


Figure B 24 *Hemimysis anomala:* cbio06 (Min Temperature of coldest month).

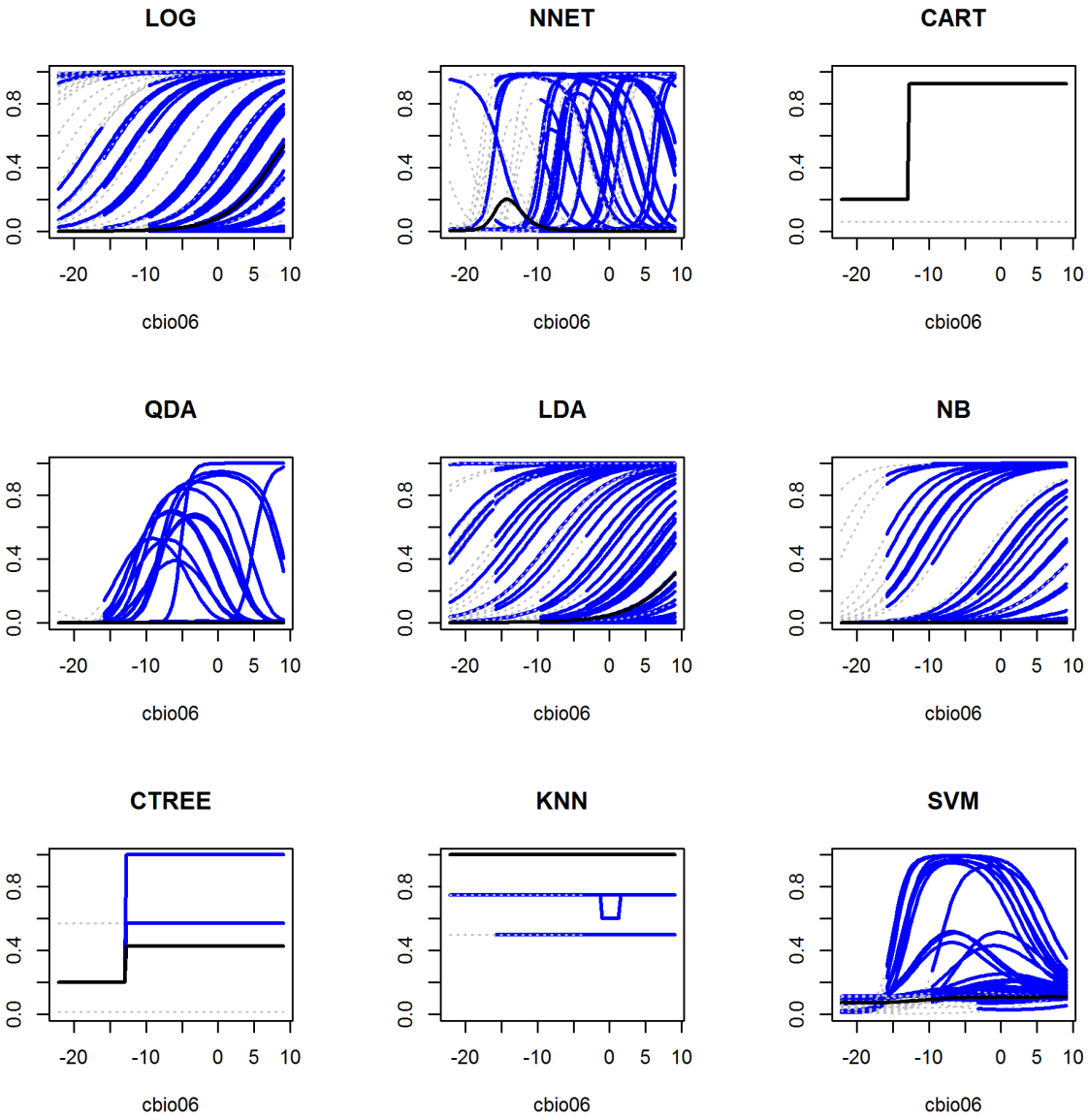


Figure B 25 *Hemimysis anomala:* cbio16 (Precipitation of the wettest quarter).

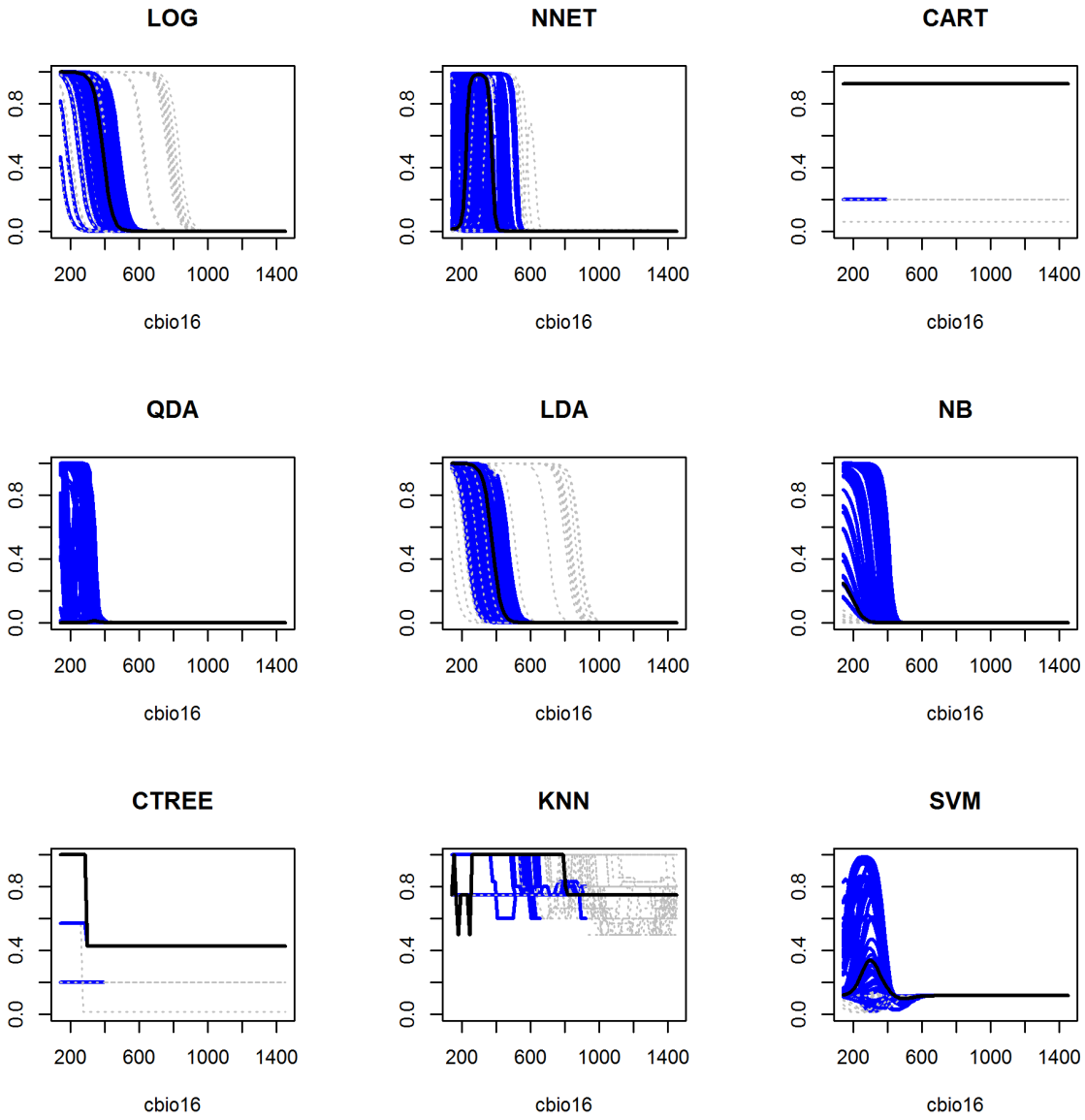


Figure B 26 *Hemimysis anomala:* cbio18 (Precipitation of the warmest quarter).

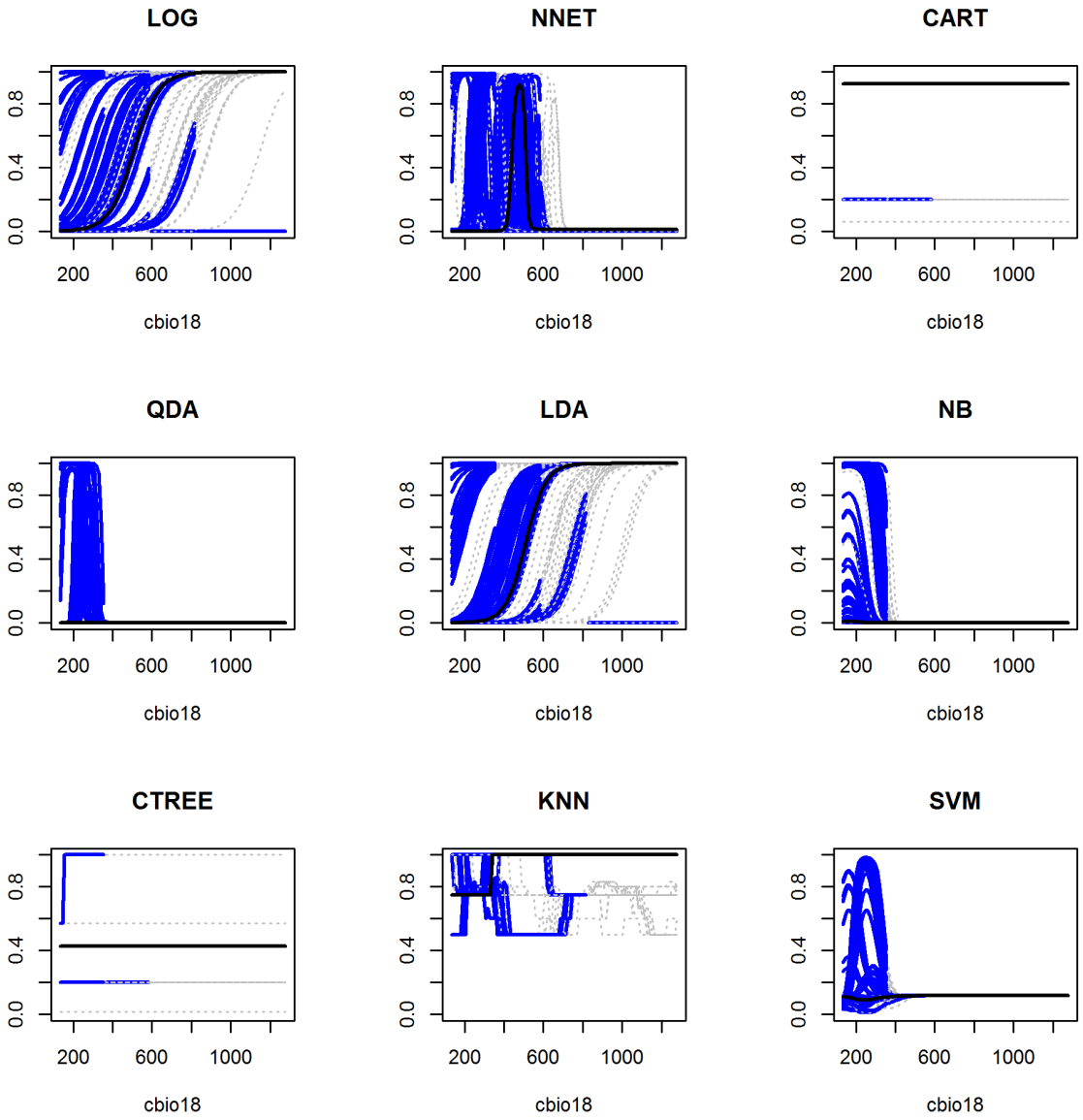


Figure B 27 *Limnoperna fortunei:* cbio05 (Max temperature of warmest month).

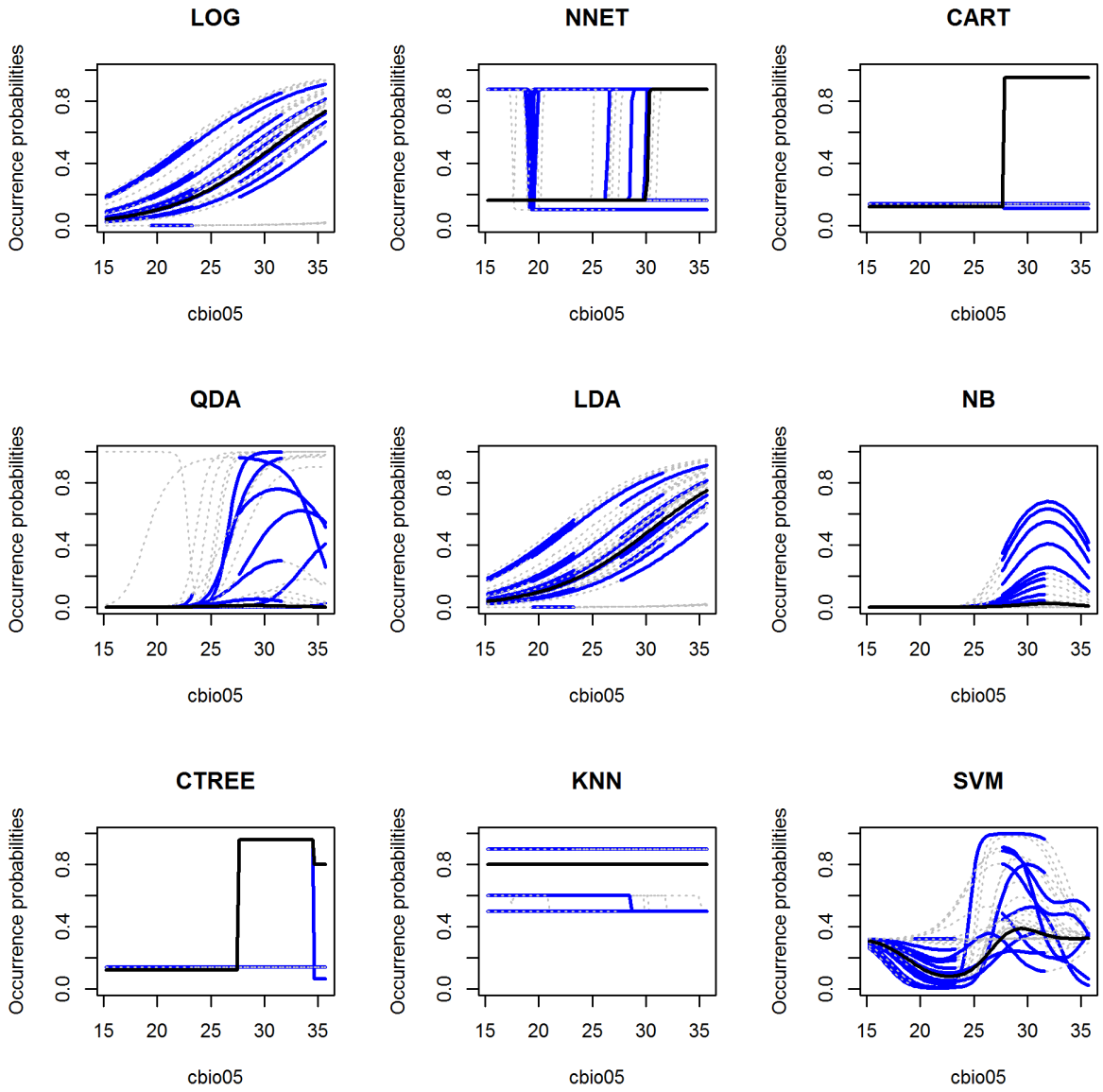


Figure B 28 *Limnoperna fortunei:* cbio10 (Mean temperature of warmest quarter).

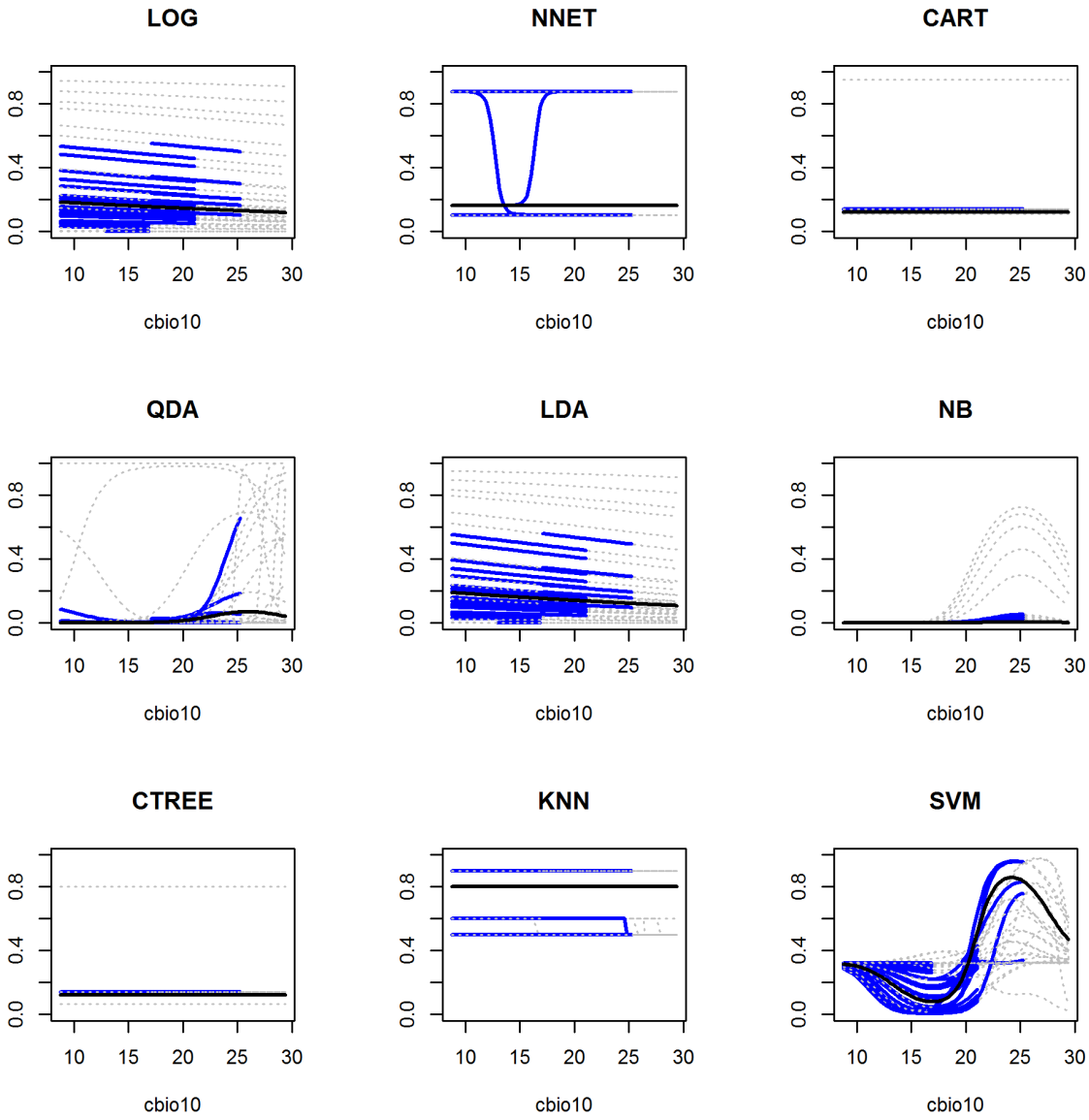


Figure B 29 *Limnoperna fortunei:* cbio12 (Annual precipitation).

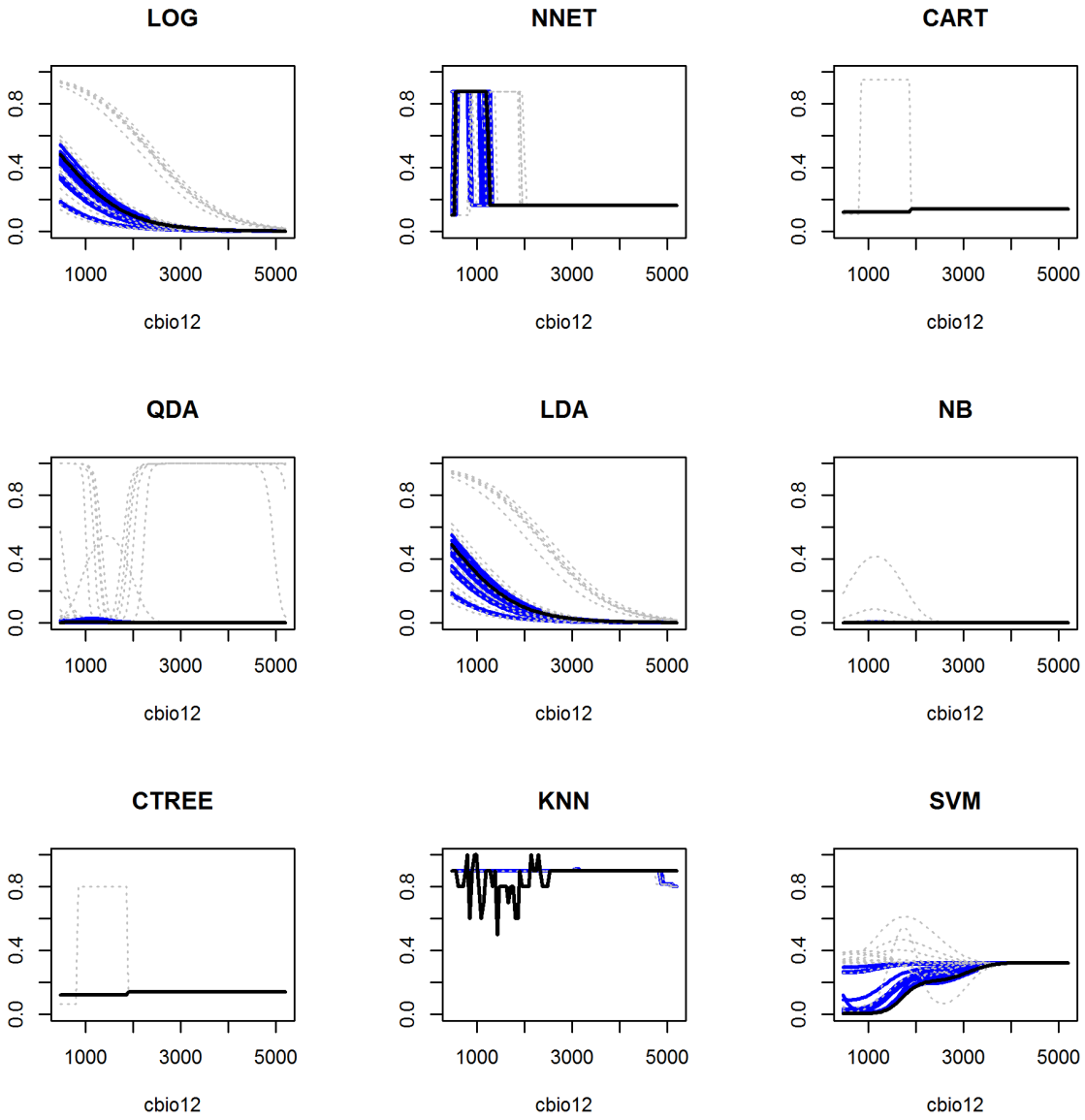


Figure B 30 *Orconectes limosus:* cbio03 (Isothermality=[temperature annual range/temperature annual range]*100).

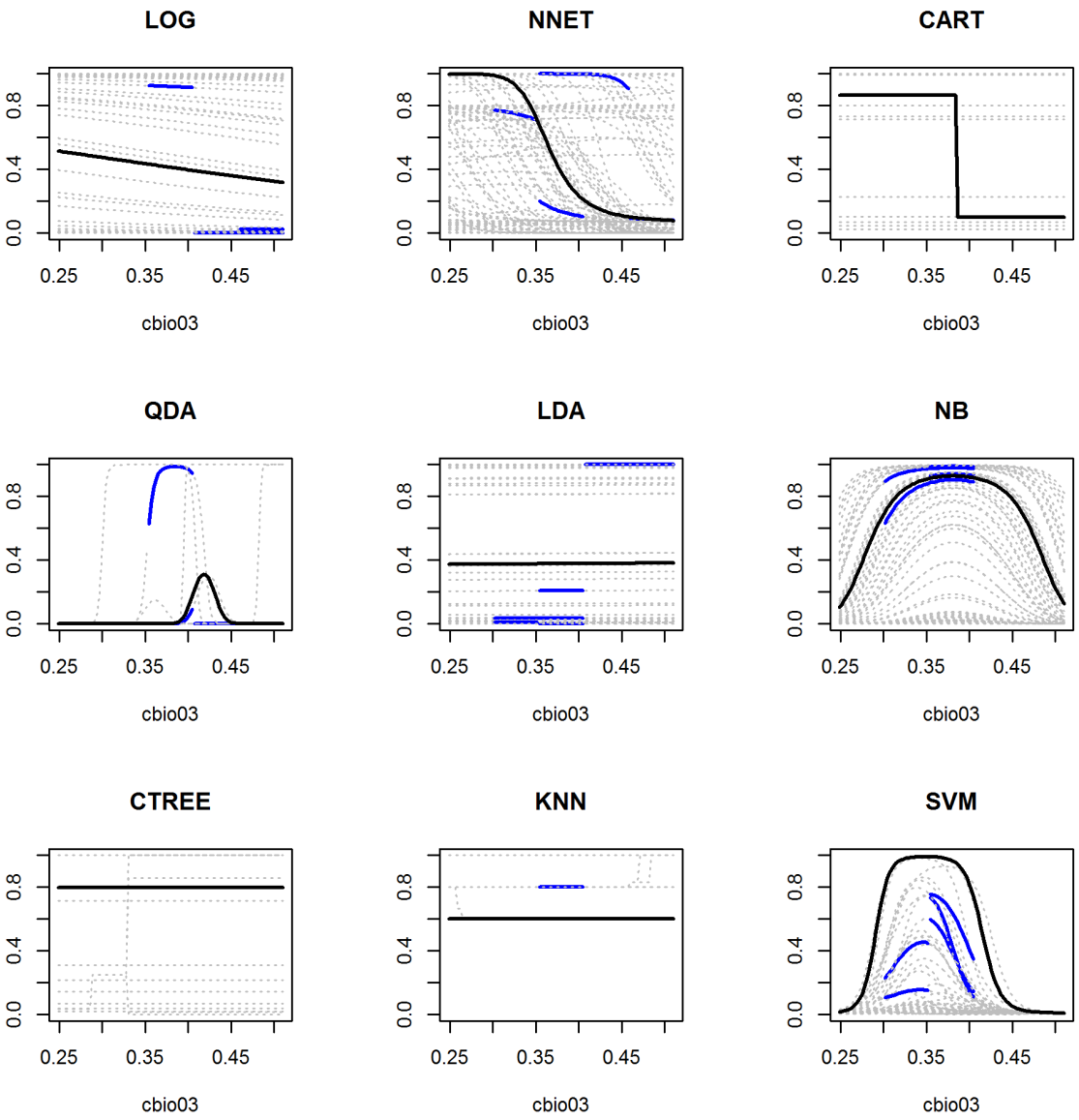


Figure B 31 *Orconectes limosus:* cbio12 (Annual precipitation).

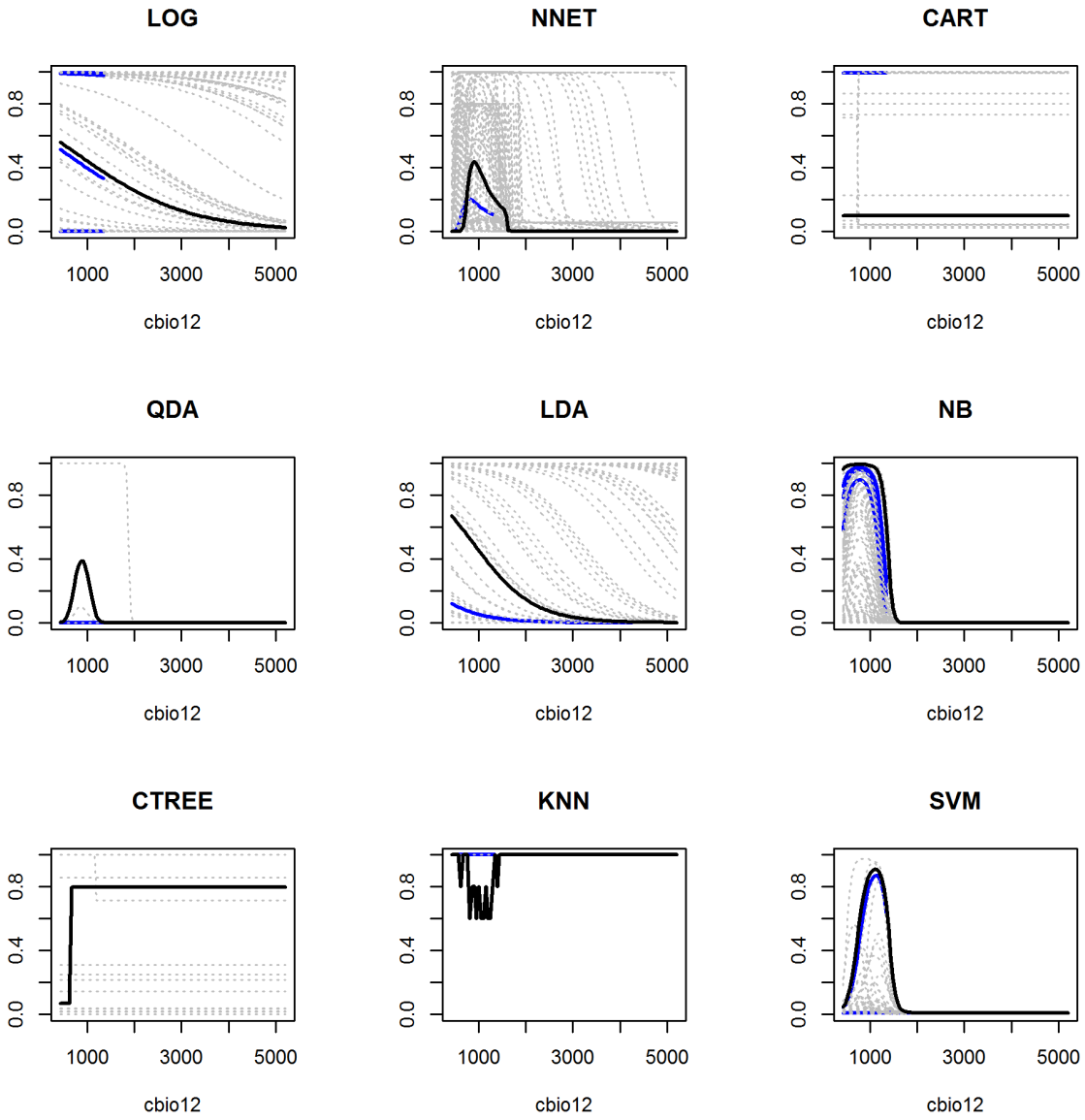


Figure B 32 *Orconectes virilis:* cbio07 (Temperature annual range).

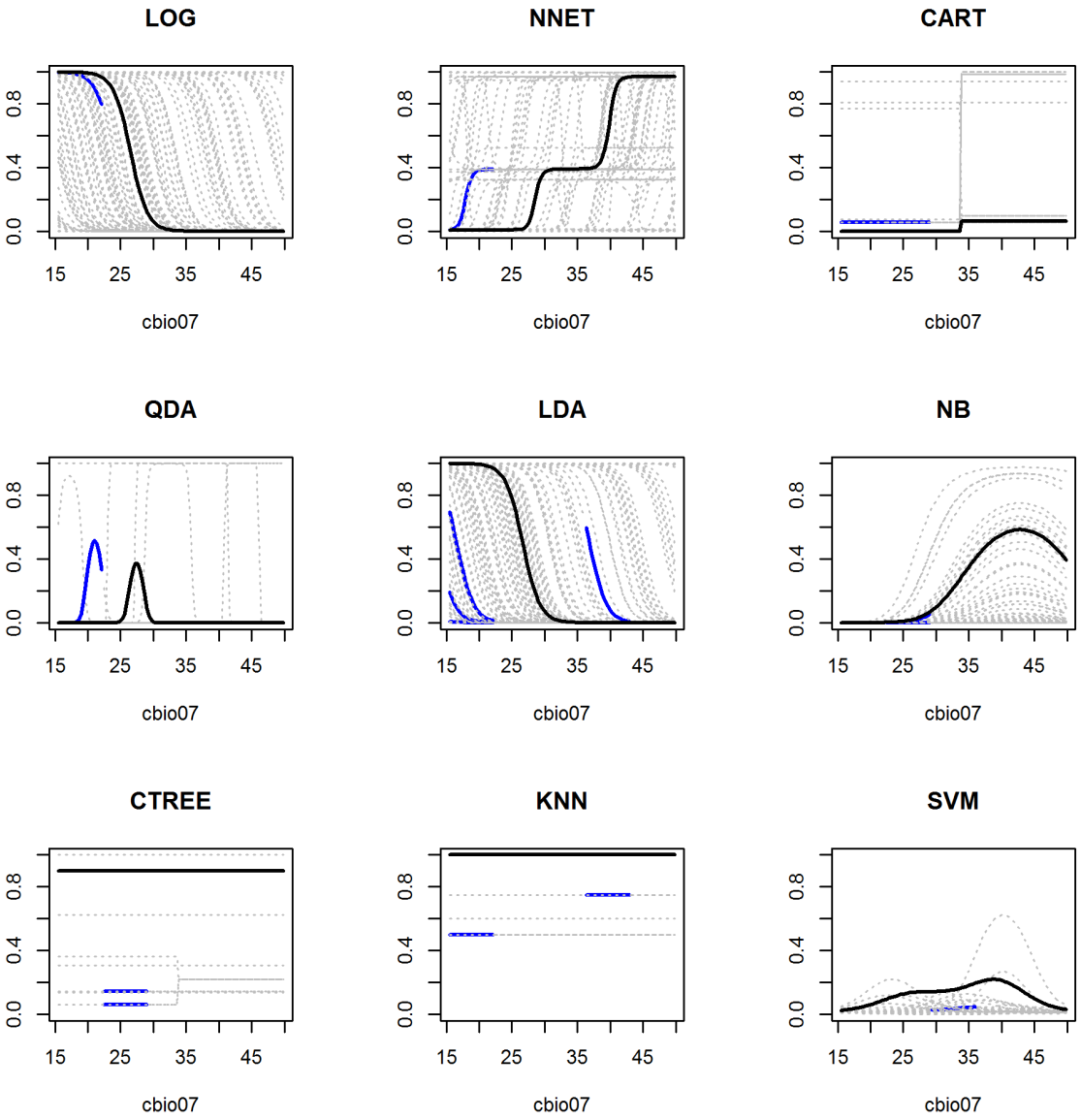


Figure B 33 *Orconectes virilis:* cbio12 (Annual precipitation).

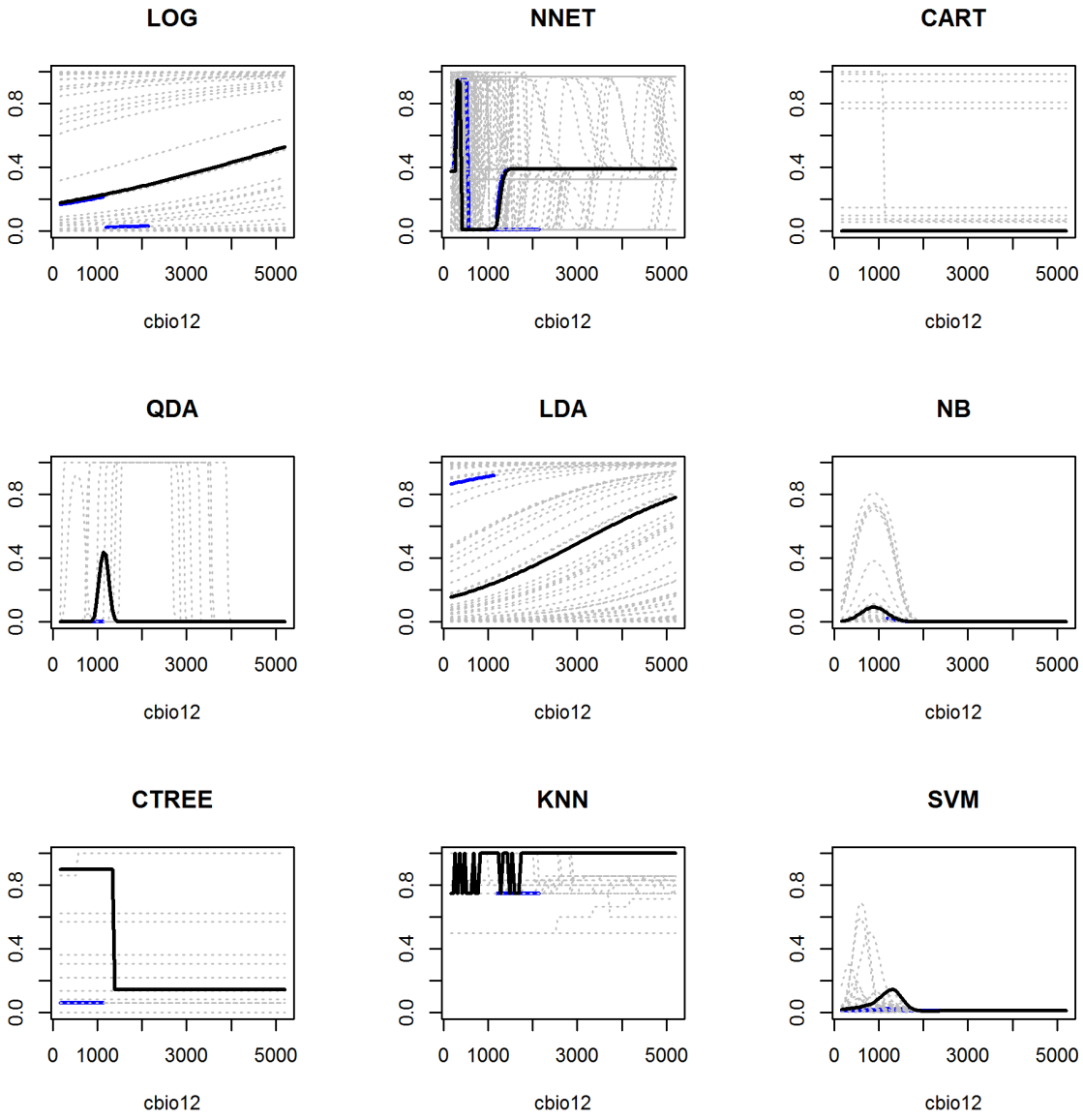


Figure B 34 *Orconectes virilis:* cbio17 (Precipitation of driest quarter).

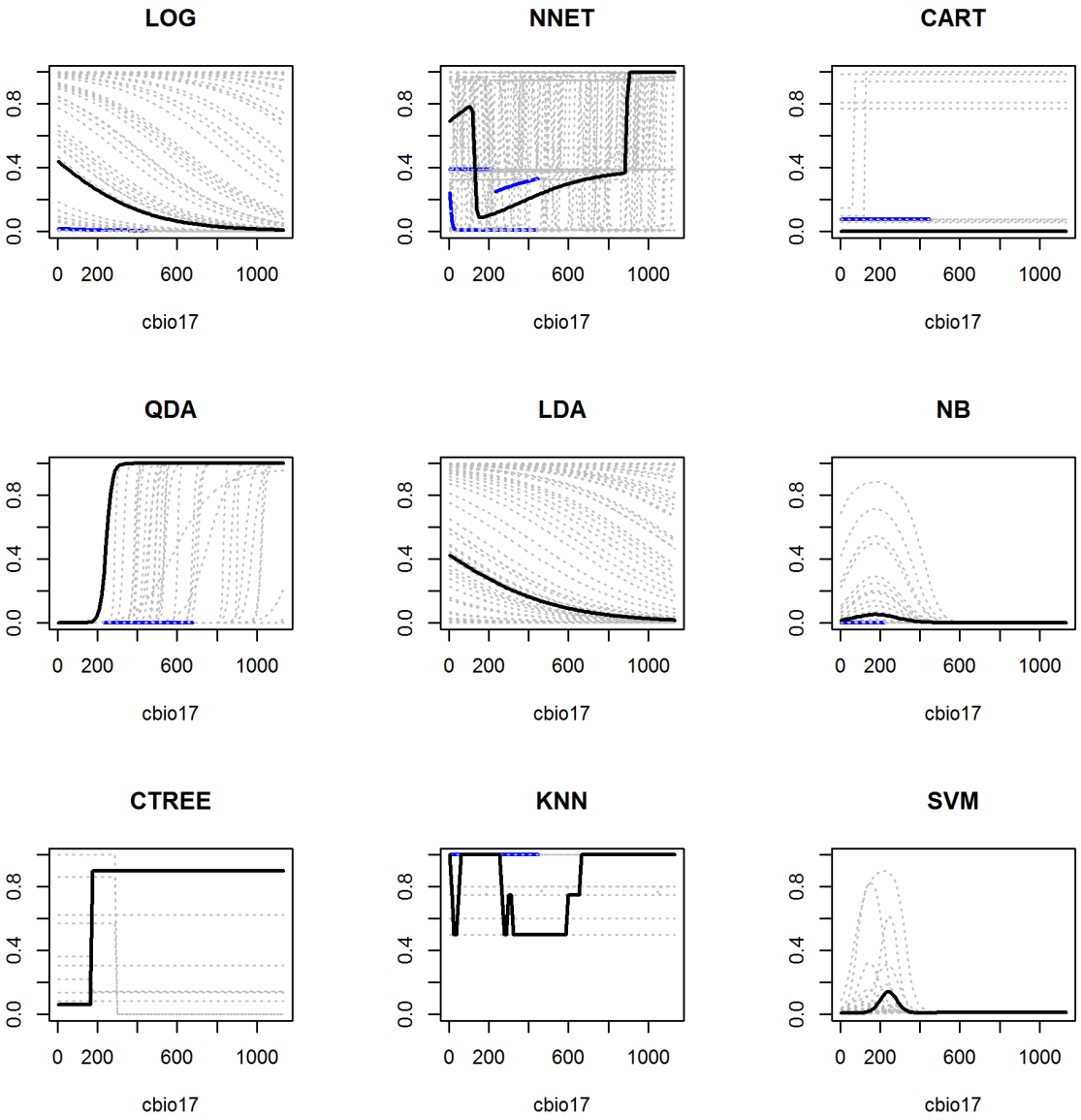


Figure B 35 *Pacifastacus leniusculus* : cbio06 (Min temperature of coldest month).

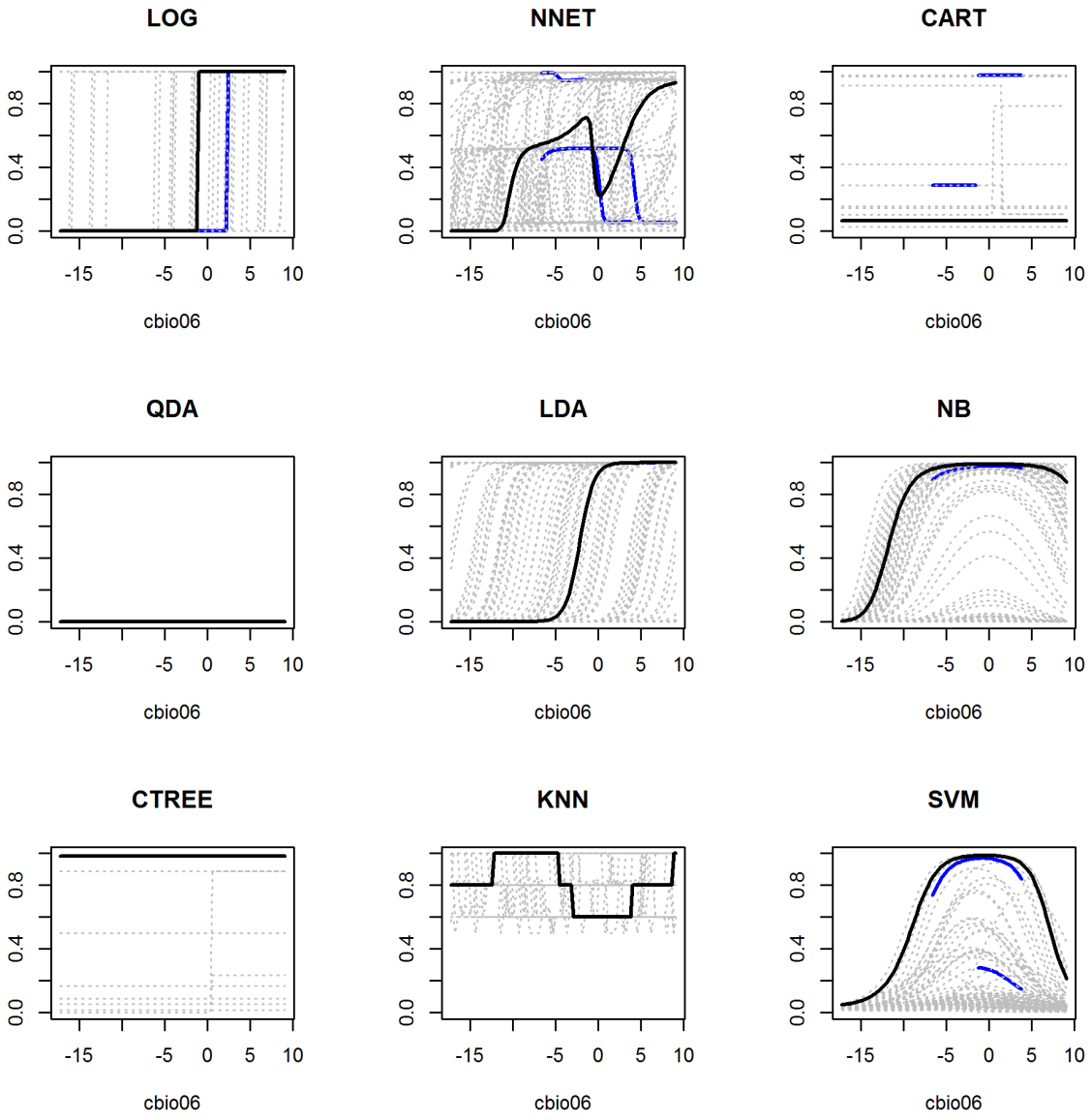


Figure B 36 *Rhithropanopeus harrisii:* cbio01 (Annual mean temperature).

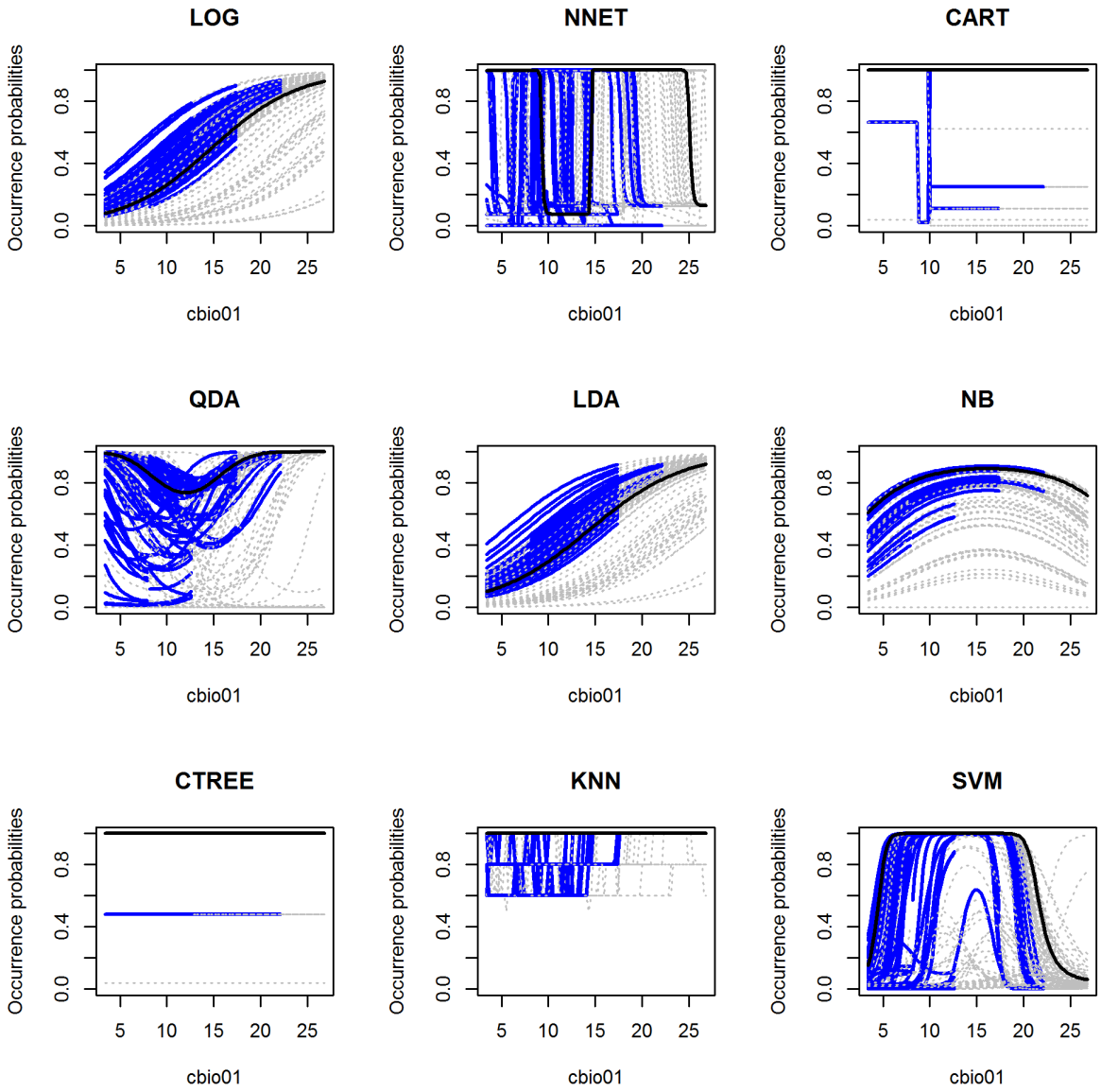


Figure B 37 *Rhithropanopeus harrisii:* cbio13 (Precipitation of wettest month).

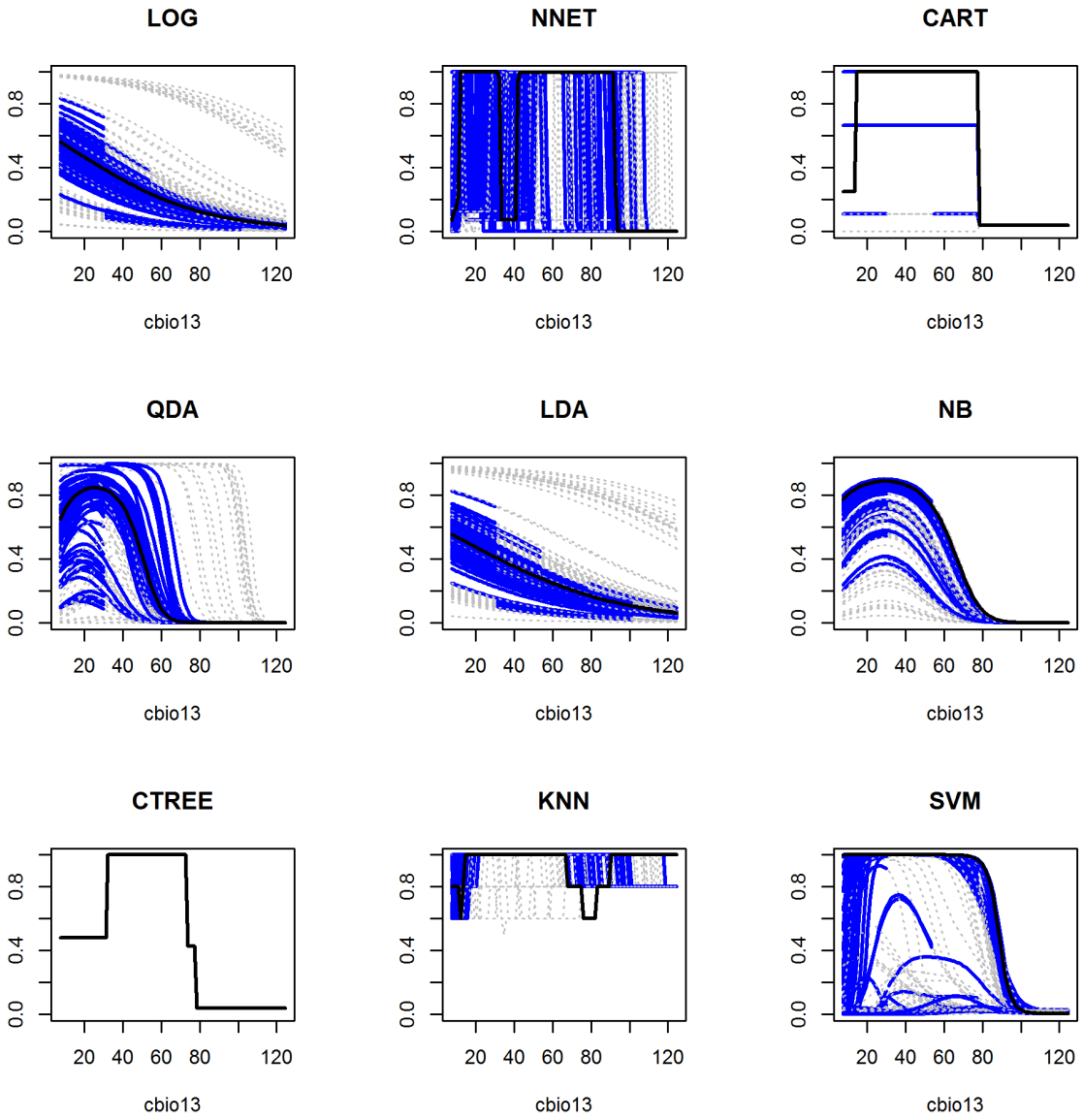


Figure B 38 *Valvata piscinalis:* cbio04 (Temperature seasonality).

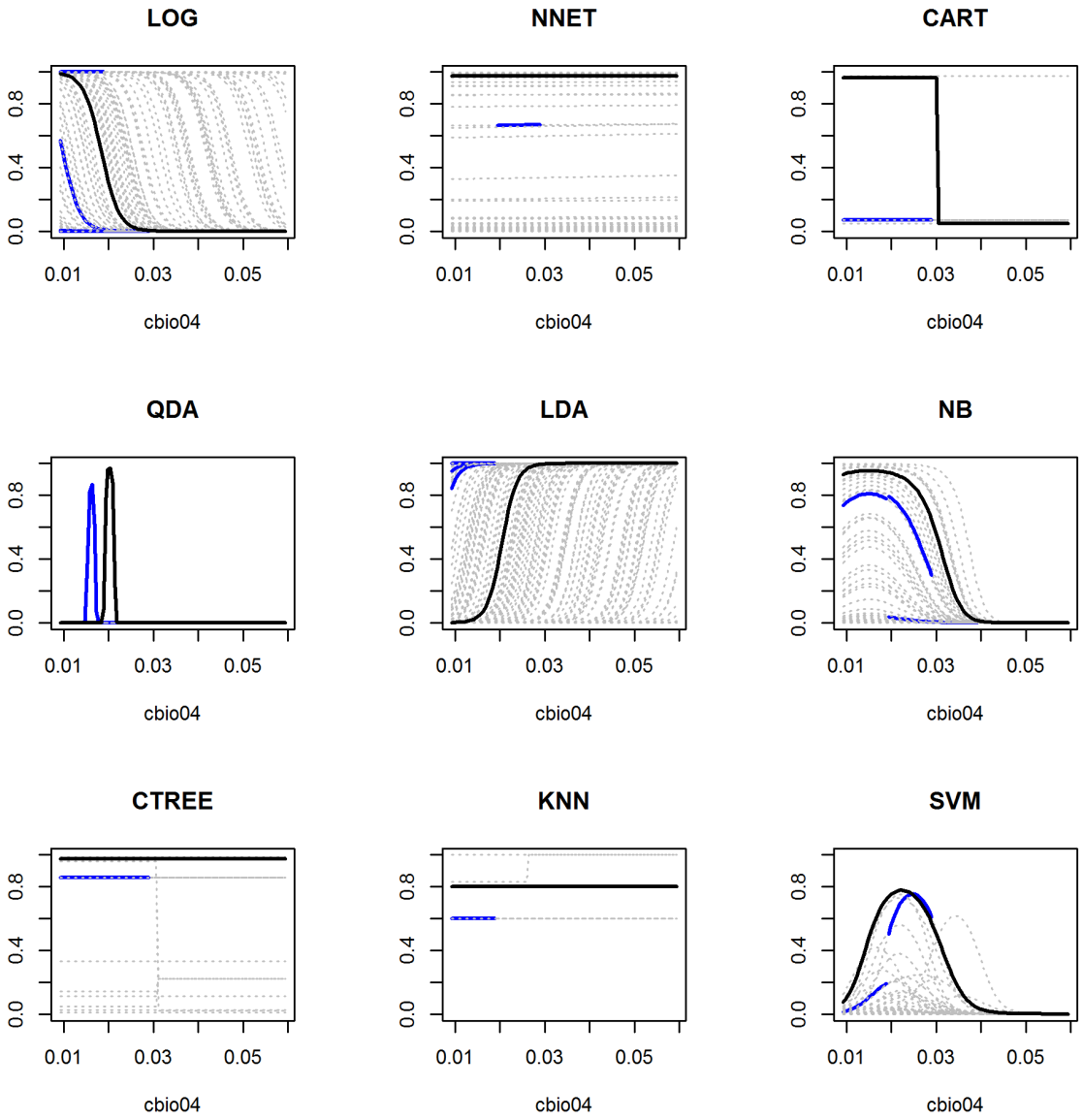
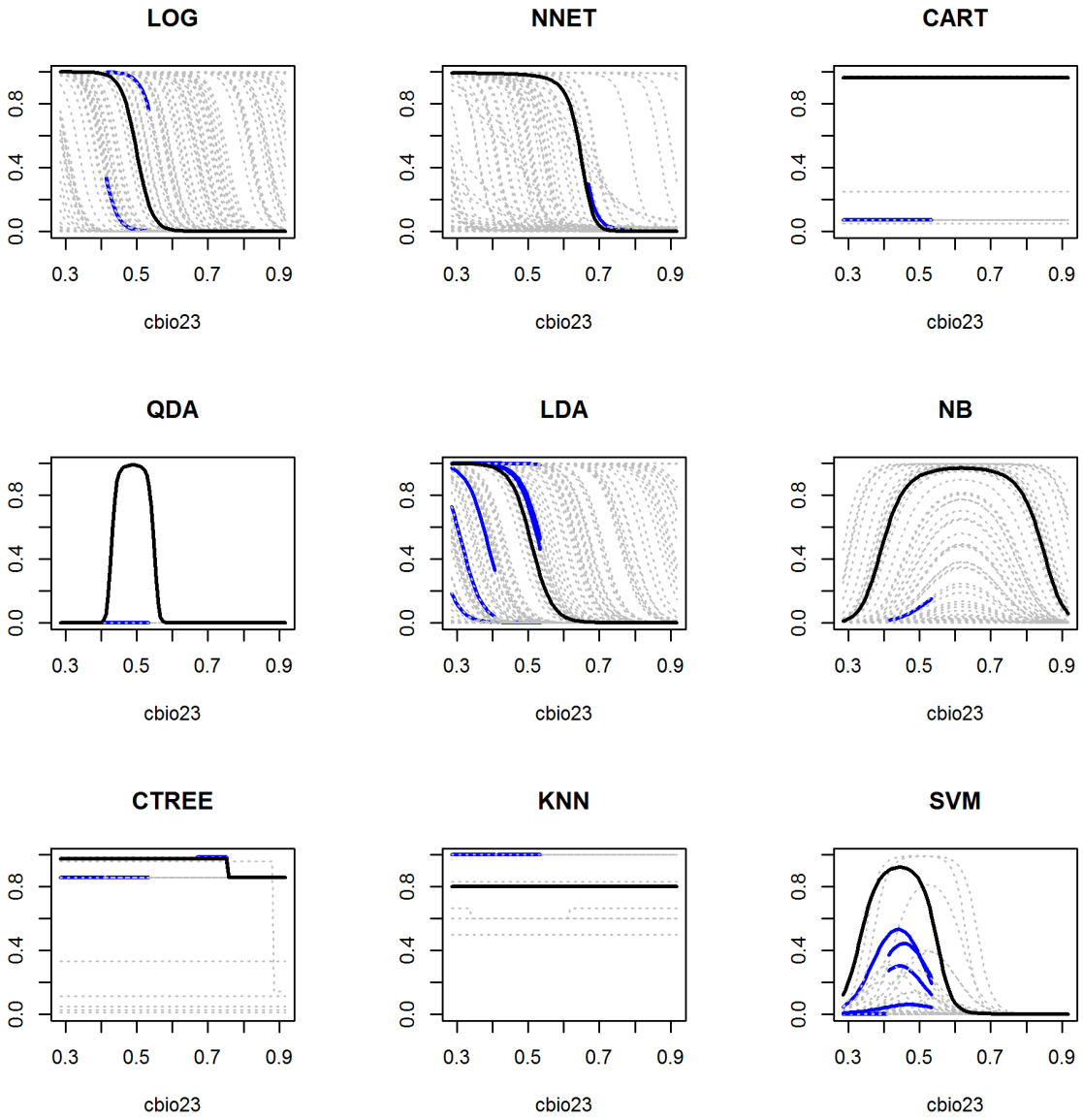


Figure B 39 *Valvata piscinalis:* cbio23 (Radiation seasonality).



B.2 AUC performance of the nine models used in the MMA framework measured 10-fold cross-validation repeated 200 times for the 21 invasive freshwater species.

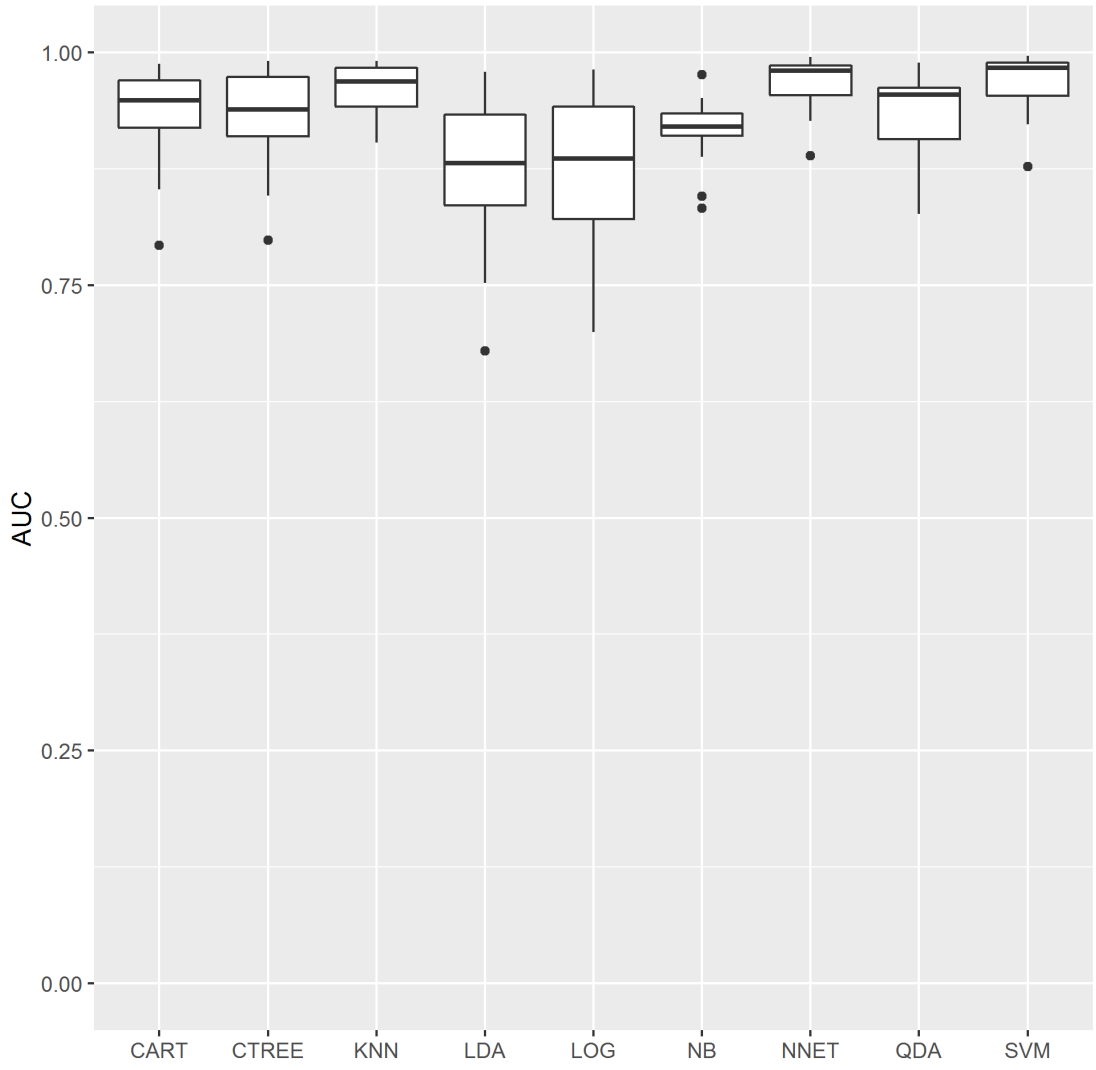


Figure B 40 AUC performance of the nine models used in the MMA framework measured by 200 10-fold cross-validation for the 21 invasive freshwater species.

Appendix C **Supplement to chapter 5**

C.1 Variables selected for each species using random forests for the three types of pseudo-absences generated. Non-masked is when the whole geographic background is used while longitudinal or latitudinal masking when part of the background is masked using longitudinal or latitudinal subsets.

Table C 1 Variables selected for each species using random forests for the three types of pseudo-absences generated. Non-masked is when the whole geographic background is used while longitudinal or latitudinal masking when part of the background is masked using longitudinal or latitudinal groups.

Species name	Non-masked	Latitudinal masking	Longitudinal masking
Aedes albopictus (Skuse, 1895)	cbio01,cbio02,cbio05,cbio06,cbio07,cbio08,cbio10,cbio11,cbio12,cbio13,cbio14,cbio15,cbio16,cbio17,cbio18,cbio19,cbio20,cbio21,cbio25	cbio06,cbio08	cbio06,cbio07
Bithynia tentaculata (Linnaeus, 1758)	cbio01,cbio02,cbio05,cbio06,cbio07,cbio09,cbio10,cbio11,cbio20,cbio21,cbio22,cbio23,cbio26,cbio27	cbio06,cbio11	cbio05,cbio08,cbio10,cbio20,cbio22,cbio26,cbio27
Bythotrephes longimanus (Leydig, 1860	cbio01,cbio03,cbio06,cbio09,cbio11,cbio18,cbio22,cbio23	cbio02,cbio03,cbio04,cbio05,cbio07,cbio08,cbio12,cbio16,cbio17,cbio18,cbio20,cbio22,cbio23	cbio01,cbio03,cbio04,cbio06,cbio11,cbio22,cbio23
Corbicula fluminea (O. F. Müller, 1774)	cbio01 ,cbio03,cbio04,cbio05,cbio07,cbio10,cbio14,cbio15,cbio17,cbio19,cbio21,cbio22,cbio23,cbio26	cbio05,cbio21	cbio05,cbio10
Dreissena bugensis (Andrusov, 1897)	cbio02,cbio03,cbio04,cbio08,cbio14,cbio17,cbio19,cbio20,cbio24	cbio01,cbio09	cbio08,cbio17
Dreissena polymorpha (Pallas, 1771)	cbio01,cbio10,cbio12,cbio18,cbio20,cbio21,cbio26	cbio01,cbio04,cbio07,cbio14,cbio17,cbio19,cbio20,cbio21,cbio26	cbio01,cbio03,cbio04,cbio06,cbio20,cbio26
Eriocheir sinensis (Milne-Edwards, 1854)	cbio01,cbio03,cbio04,cbio06,cbio07,cbio08,cbio09,cbio10,cbio11,cbio12,cbio14,cbio19,cbio25	cbio01,cbio02,cbio04,cbio07,cbio22,cbio24,cbio26	cbio01,cbio02,cbio04,cbio07,cbio10,cbio22,cbio23,cbio26,cbio27
Gammarus tigrinus (Sexton, 1939)	cbio01,cbio02,cbio07,cbio15,cbio21,cbio26	cbio04,cbio06,cbio07,cbio09,cbio11,cbio20,cbio21	cbio02,cbio06,cbio07,cbio20,cbio21,cbio22,cbio23,cbio26,cbio27
Orconectes limosus (Rafinesque, 1817)	cbio01,cbio03,cbio04,cbio05,cbio10,cbio12,cbio20,cbio23,cbio27	cbio01,cbio06,cbio11	cbio01,cbio05,cbio10
Orconectes virilis (Hagen, 1870)	cbio04,cbio05,cbio07,cbio08,cbio09,cbio10,cbio12,cbio17,cbio18,cbio25	cbio04,cbio23	cbio04,cbio05,cbio15,cbio21,cbio22,cbio24,cbio26
Pacifastacus leniusculus (Dana, 1852)	cbio01,cbio04,cbio05,cbio06,cbio07,cbio10,cbio15,cbio22,cbio23,cbio27	cbio03,cbio04,cbio06,cbio07,cbio11,cbio18,cbio24,cbio26	cbio01,cbio04,cbio10,cbio20,cbio22,cbio23,cbio27
Pomacea canaliculata (Lamarck, 1828)	cbio01,cbio05,cbio06,cbio07,cbio08,cbio09,cbio10,cbio11,cbio13,cbio19	cbio21,cbio26	cbio02,cbio08
Procambarus clarkii (Girard, 1852)	cbio01,cbio06,cbio11,cbio13,cbio22,cbio23,cbio27	cbio01,cbio02,cbio06,cbio11,cbio20	cbio01,cbio04,cbio05,cbio06,cbio07,cbio08,cbio10,cbio11,cbio20
Valvata piscinalis (Muller, 1774)	cbio02 ,cbio04,cbio05,cbio07,cbio10,cbio20,cbio22,cbio23,cbio26,cbio27	cbio03,cbio04,cbio06,cbio07,cbio08,cbio09,cbio11,cbio23,cbio24	cbio11,cbio20,cbio21,cbio22,cbio23,cbio26,cbio27

C.2 Final model parameters used for KNN, SVM and NNET obtained by testing different sets of parameters (Appendix A.4) using cross-validation.

Table C 2 Parameters selected for the non-masked background datasets.

Model	KNN	SVM		NNET		
Species	k	C	sigma	Size	Maxiter	Decay
Aedes albopictus (Skuse, 1895)	4	100	0.9	5	1000	0.01
Bithynia tentaculata (Linnaeus, 1758)	4	100	0.9	5	1250	0.001
Bythotrephes longimanus (Leydig, 1860)	5	100	0.9	5	1000	0.01
Corbicula fluminea (O. F. Müller, 1774)	4	100	0.7	5	1000	0.01
Dreissena polymorpha (Pallas, 1771)	5	100	0.9	5	750	0.01
Dreissena rostriformis bugensis (Andrusov, 1897)	5	100	0.9	5	1000	0.01
Eriocheir sinensis (Milne-Edwards, 1854)	4	100	0.9	5	750	0.01
Gammarus tigrinus (Sexton, 1939)	4	100	0.9	5	1500	0.01
Orconectes limosus (Rafinesque, 1817)	4	100	0.9	5	500	0.01
Orconectes virilis (Hagen, 1870)	5	100	0.9	5	750	0.01
Pacifastacus leniusculus (Dana, 1852)	4	100	0.9	5	750	0.01
Pomacea canaliculata (Lamarck, 1828)	5	100	0.9	5	500	0.01
Procambarus clarkii (Girard, 1852)	5	100	0.9	5	1000	0.01
Valvata piscinalis (Muller, 1774)	5	100	0.9	5	500	0.01

Table C 3 Parameters selected for the longitudinal masked background datasets.

Model	KNN	SVM		NNET		
Species	k	C	sigma	Size	Maxiter	Decay
Aedes albopictus (Skuse, 1895)	19	100	0.9	5	750	0.01
Bithynia tentaculata (Linnaeus, 1758)	19	100	0.9	5	500	0.01
Bythotrephes longimanus (Leydig, 1860)	9	100	0.9	5	1250	0.01
Corbicula fluminea (O. F. Müller, 1774)	20	100	0.9	5	1500	0.001
Dreissena polymorpha (Pallas, 1771)	20	100	0.9	5	1000	0.01
Dreissena rostriformis bugensis (Andrusov, 1897)	18	100	0.9	5	1500	0.01
Eriocheir sinensis (Milne-Edwards, 1854)	7	100	0.9	5	1000	0.01
Gammarus tigrinus (Sexton, 1939)	9	100	0.9	5	1250	0.01
Orconectes limosus (Rafinesque, 1817)	15	100	0.9	5	500	0.01
Orconectes virilis (Hagen, 1870)	19	100	0.9	5	1500	0.01
Pacifastacus leniusculus (Dana, 1852)	9	100	0.9	5	500	0.01
Pomacea canaliculata (Lamarck, 1828)	17	100	0.9	5	1250	1.00E-04
Procambarus clarkii (Girard, 1852)	13	100	0.9	5	750	0.01
Valvata piscinalis (Muller, 1774)	13	100	0.9	5	1500	0.01

Table C 4 Parameters selected for the latitudinal masked background datasets.

Model	KNN	SVM		NNET		
Species	k	C	sigma	Size	Maxiter	Decay
Aedes albopictus (Skuse, 1895)	19	100	0.9	5	1000	0.001
Bithynia tentaculata (Linnaeus, 1758)	19	100	0.9	5	750	1.00E-04
Bythotrephes longimanus (Leydig, 1860)	13	100	0.9	5	500	0.01
Corbicula fluminea (O. F. Müller, 1774)	19	100	0.9	5	750	0.01
Dreissena polymorpha (Pallas, 1771)	13	100	0.9	5	1250	0.01
Dreissena rostriformis bugensis (Andrusov, 1897)	8	100	0.9	5	1000	1.00E-04
Eriocheir sinensis (Milne-Edwards, 1854)	9	100	0.9	5	1000	0.01
Gammarus tigrinus (Sexton, 1939)	7	100	0.9	5	1250	0.001
Orconectes limosus (Rafinesque, 1817)	15	100	0.9	5	1000	0.01
Orconectes virilis (Hagen, 1870)	17	100	0.9	5	1250	0.01
Pacifastacus leniusculus (Dana, 1852)	5	100	0.9	5	1000	0.01
Pomacea canaliculata (Lamarck, 1828)	4	100	0.9	5	1250	0.01
Procambarus clarkii (Girard, 1852)	13	100	0.9	5	1500	0.01
Valvata piscinalis (Muller, 1774)	19	100	0.9	5	500	0.01

C.3 Coefficient estimates (effect size) for the fixed effect variables with parametric bootstrap 95% confidence interval from the linear mixed model. The response variable was model performance and the fixed effects were pseudo-absences, evaluation and modelling techniques. Only the fixed effects pseudo-absence and evaluation method are shown here as they were the effects of interest. The effect sizes are compared to a reference, which is non-masked pseudo-absence technique and random cross-validation evaluation technique. Confidence intervals not overlapping with zero indicate a significant difference with the reference. nrcv (non-random cross-validation). Three model performance metrics were tested in addition to RMSE, AUC, kappa and tss.

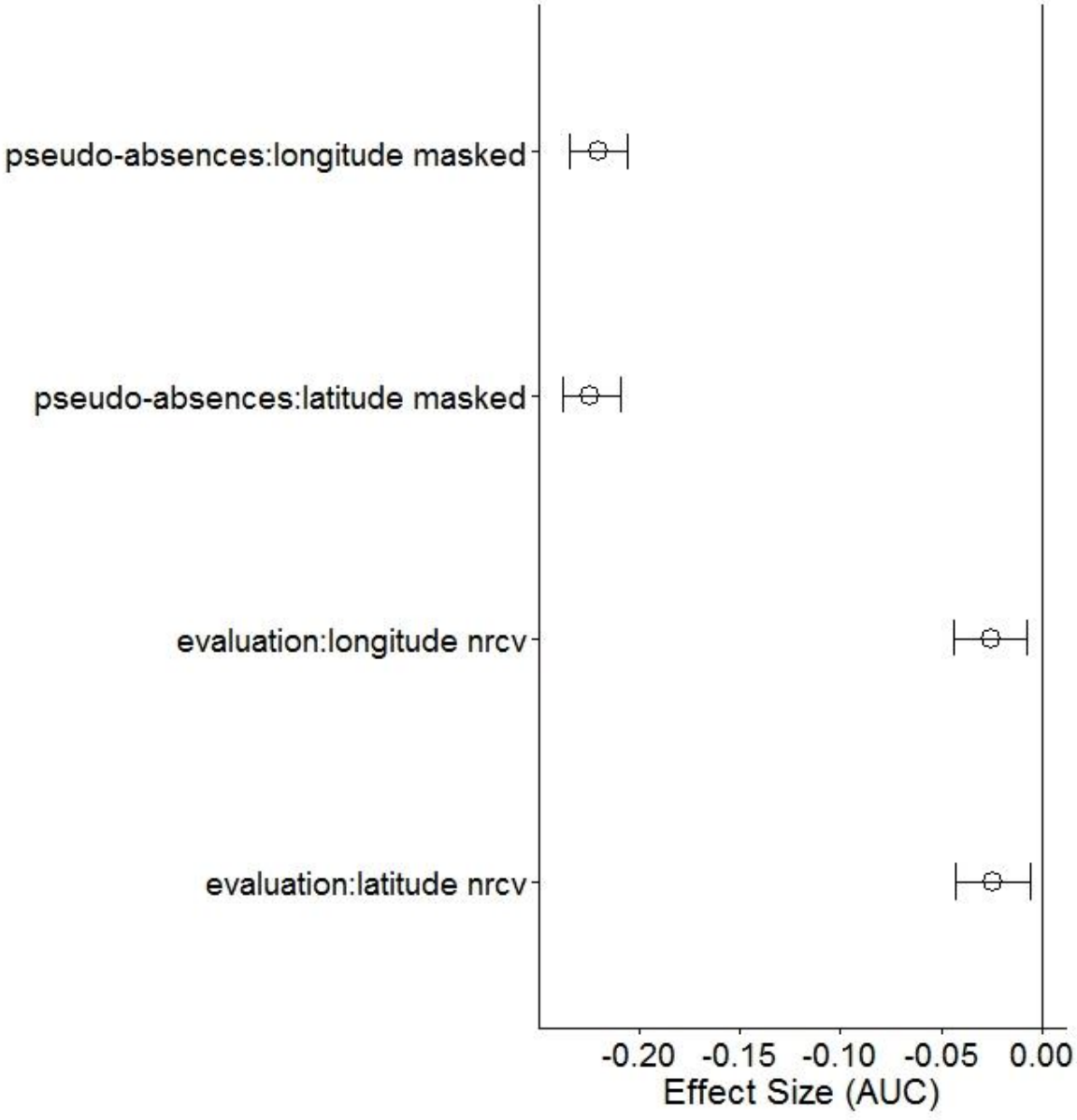


Figure C 1 AUC (Area under a ROC curve) (Fielding & Bell, 1997). The average and 95% confidence interval of the reference category was 0.84 [0.81, 0.88].

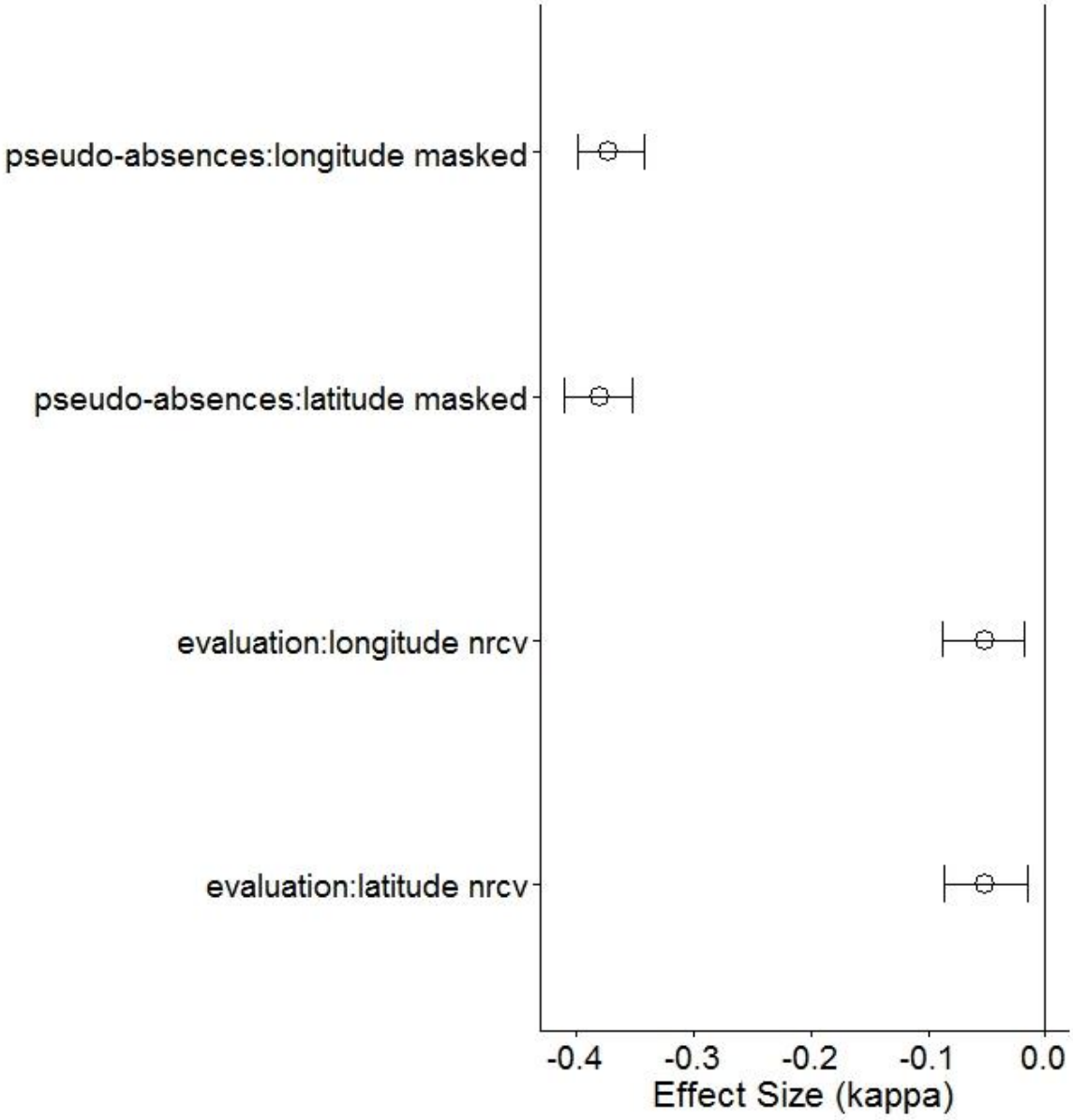


Figure C 2 Kappa (Liu et al., 2009). The average and 95% confidence interval of the reference category was 0.55 [0.49, 0.62].

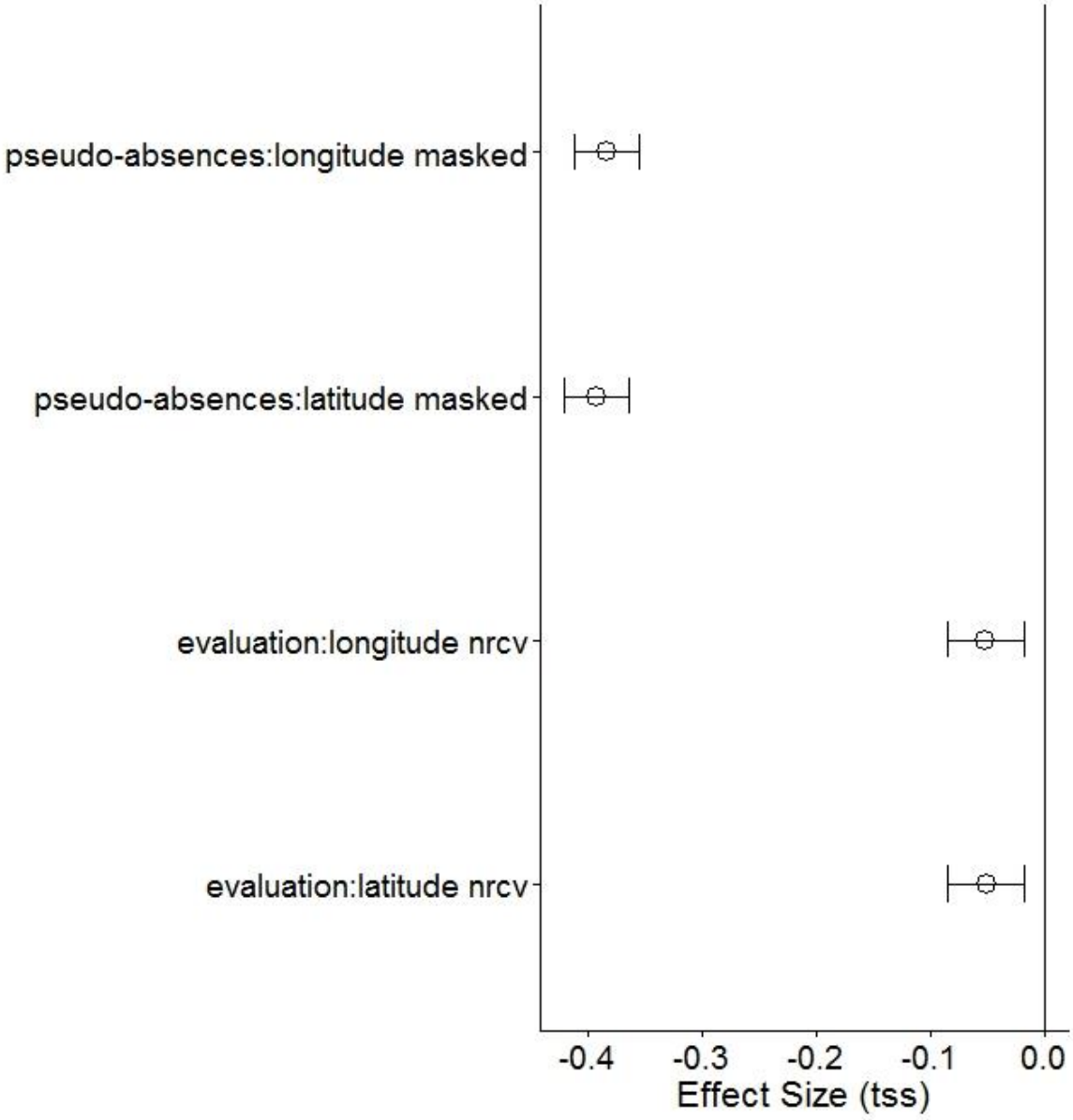


Figure C 3 Tss (true skill statistic) (Liu et al., 2009). The average and 95% confidence interval of the reference category was 0.57 [0.51, 0.64].

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